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L. BOROSS, O. FEHÉR, L. FERENCZY, I. HORVÁTH, ERZSÉBET KÖVES,
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MÓCZÁR L., OROSZ L., SZALAY L.

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COMMEMORATION OF JÓZSEF GELEI, ON THE OCCASION OF THE TWENTY—FITFH ANNIVERSARY OF HIS DEATH*

I have received the honourable task of erecting a monument, for the second time, to the memory of an illustrious predecessor and friend, the academician Dr. JÓZSEF GELEI, professor of the University in Szeged. I say: "for the second time" because I paid homage and expressed my devotion to him when we surrounded his coffin and — remembering a breath-taking folk-song, the "Blue forget-menot" sung by him and his students in the train, on the occasion of his last study-tour, as if bidding a last farewell to us — among the dun-coloured clods of earth I saw a bunch of wood forget-me-not flying towards the coffin which separated him from us, definitely and for ever. Who JÓZSEF GELEI was, was and is known by anybody who has ever made approaches to him, having the privilege of listening to the explanations of

* Address delivered by the author at session 34 of the "Scientific Sessions of the Academy Committee in Szeged and University Medical School in Szeged 1976/1977", on November 22, 1977.

his profound ideas arranged in exact sentences on the thesaurus of nature whose doors, openable only with much work and love, he did frequently open before those longing for knowledge and thirsting to obtain it. He was a man, a man of great sensitivity, a natural scientist saturated with a deep and unselfish love of science, who made his mark on the history of biology and is thought of with revence by anybody who enjoyed — even if only once — the humanism bursting out of him and that splendid spirit given only to exceptional individuals.

He was born at Árkos, in County Háromszék, on August 20, 1885. His father was a smallholder whose hands were often chapped by the stilt of plough, the snath, and the axe-helve. His will was seasoned by the time. He was brought up by the summits towering to the sky, the talkative springlets, the whispering pine-woods, by the oak-trees facing the storm and the multiform flowers opening their petals one after the other on the plot of grass of the woodland-clearing, to be a sensitive, trustful, and considerate man. He was taught among forked lightning, and by the dark clouds of hailstorms that man is an obedient tool of the great nature, struggling with an unsurpassable might. And he also learned that to the mountains which cannot be approached without toilsome work one must return, because at a great hught the wind is cool and the evening comes early. At this school the child JÓZSEF GELEI, was also educated. Here he learned to know, admire and love the great nature, and to trust in intellect which protects us from dangers if we have enough of it. Anybody knowing JÓZSEF GELEI well had to find sooner or later, that this was the background determining his deeds, governing the course of his life, and providing encouragement and help to his everyday conduct. In this school he also learned that all others are human beings, too, and that nobody is either entitled to contemn, nor obliged to look up to, others.

He finished his primary schooling at Árkos, his grammar-school studies in Kolozsvár, taking his final examination in 1903. Then he was matriculated to the Faculty of Mathematics and Natural Sciences of the University in Kolozsvár, for Studying of natural history and chemistry. Of his teachers, the one who made the greates effect on him was the professor of zoology, ISTVÁN APÁTHY who, recognizing the particular interest of the ambitious boy in zoology and particularly in histology and cytology, had him appointed to demonstrator in the Institute of Zoology and Comparative Anatomy in the University in 1905. In this way, an opportunity was provided for him to work under excellent conditions practically unrivalled in the world at that time. Before long, he became professor's assistant and worked in this capacity until 1912. His doctoral thesis was made on an animal belonging to the freeliving flatworms (Turbellaria): the *Olisthanella hungarica*, discovered by him in the waters in the neighbourhood of Kolozsvár. With this paper he became "engaged" to the Turbellaria and in the course of investigating these he enriched the systematic and anatomical literature concerning this animal group with a number of productions of imperishable value. In the course of this activity the spiritual complexion of a meditating inquiring biologist took shape in him with the ever determined endeavour to look for the place and explanation of every biological phenomenon in the function of the cell, and to resort exclusively to the cell in order to understand the biological phenomena. Here, beside his master, he became while still young a histologist, a microtechnicist and one of the early cytologists producing preparations with his simplest tools, that are looked on with admiration even in the age of the electron microscope.

In order to enable him to obtain a deeper insight into the problems concerning the life and structure of the species belonging to Turbellaria, in 1906 ISTVÁN APÁTHY sent him to Graz, to the professor, of Hungarian origin, LAJOS GRAFF, where he spent a year. During this time not only did his vision broaden considerably but also his knowledge concerning the animal groups increased and gained strength. As his principal, as well as he himself, were primarily interested in histology, and later cytology, of animals and in the genetic relations of these, he chose for the object of his research work the easily accessible large flatworm, the milk-white turbellarian *(Dendrocoelum lacteum)*.

In 1911, he spent a year in Munich, in the Institute of RICHARD HERTWIG who was not only a researcher of repute and of a wide field of interest but also an excellent teacher and Head of Department, from whom he could learn much in many areas and in whose great and well-equipped Institute he could work comfortably.

In 1912, also for a year, he stayed in Würzburg in Boveri's Institute and from him he learned much, particularly concerning experimental approaches. He also made a great impression on BOVERI with his microtechnical knowledge and his particular practical sense. Here he continued the histological and cytological investigations into Dendrocoelum which later resulted in the recognition of the longitudinal pairing of chromosomes.

From 1912, he was working in Apáthy's Institute as a middle school teacher, holding there a subordinate post where he could deal, free from any administrative work, with exclusively scientific research work.

In 1914, he obtained the qualification of privat-docent of the University in "comparative cytology" and in this quality, too, he continued functioning as a subordinate teacher in Apáthy's Institute until 1919 when he was appointed teacher of the Unitarian grammar-school in Kolozsvár.

Somewhat interrupting the course of what I have to say, let me mention that only now as I am writing my commemoration do I understand why JÓZSEF GELEI loved ISTVÁN APÁTHY so much and looked up to him, why he always spoke of him with an unsurpassable admiration, his face assuming an expression of transfiguration when, during our conversations, there was any talk of him in any context. So far, I have only known of ISTVÁN APÁTHY that he was an excellent neurohistologist, an unequalled microtechnicist and an unshakeable protagonist of the continuous connection between neurons, the continuity. I had no idea of that he was such a careful educator, such a long-sighted leading personality, so high on the top of his vocation. At any rate, had I known this about him, then I should have mentioned this, in my written commemorations about him, as his highest merit.

The year 1924 brought a large change in József Gelei's life when he was appointed to the chair of the Department of General Zoology and Comparative Anatomy, in Szeged. He had to leave Kolozsvár where he had spent his young years, had become a slave to science, a highly competent researcher and a devoted of nature. He had to leave the river great Szamos in which, as told by himself, he had learned swimming after being pushed by somebody from the riverside into the water, suddenly and unobserved. He had to leave the glorious Institute where there was peace, work had its honour, and man was considered as man by the others. In Szeged he was received by a great vacuum and great poverty. The Institute of Zoology and Comparative Anatomy of the University, the Director of which he became, found

provisional place in a middle school, scantily and without any equipment. The terrible conditions not only impeded any considerable research work but also induced great deficiencies in instruction. Luckily, the situation changed before long. He obtained a spacious, clear, large Institute consisting of several fine premises. As Rockefellers material subsidy duly arrived, he was able to organize such a superb, well-designed Institute, suitable both to the requirements of instruction and to those of scientific research work, that in the range of experimental zoological institutes it stood all the demands of the first place, even if judged by foreign standards. Everything contained in it, as it was arranged, demonstrated that the organizer was well beyond the capacities of this country and what he had learned there, as he produced at home something far better than it had been. If there was any failure in this Institute — it was that there were very few students. Not only did the places established for foreign research workers remained unclaimed, but there were hardly any researchers for the positions belonging to the Institute.

After the return of Transylvania, the University, which had escaped from Kolozsvár to Szeged, returned to Kolozsvár. But, as is known well enough, in 1944 it had to leave Kolozsvár again in such a way that even the books, equipments and instruments remained there, without exception. JÓZSEF GELEI left for Szeged. As, however, the Chair in the Szeged University was occupied, he drew back for a time to his farmstead in the neighbourhood of Szeged, running there an intensive farming on the „blessed" sand, as he called is. After a few years, however, a Biological Department was organized in the Medical Faculty of the University in Szeged and JÓZSEF GELEI was invited and appointed to the Chair. At first, he was given a room in the Institute of Anatomy where, without co-workers and equipment, he had to be content with lecturing to his students. Later on, upon the request of the Medical Faculty, we placed at his disposal a few rooms which he developed a well-functioning institute, supplied well both from the points of view of personnel and instruments. When this Institute began setting to work, although he was still far short of the usual age limit, he was reminded by some serious pathological changes to be sparing with „oil" and „work". Work however is not only a feeling of want but an everyday need, medicine and consolation for anybody who was born to work and enjoys doing it. GELEI went on with working and the oak facing the storm was felled by the implacable disease. The floating wick, when its flames gave light to others, burned itself, as well.

If — after the foregoing — I have to give an account of everything done by JÓZSEF GELEI in the field of science — and I feel it my duty to do so — then I have to differentiate — as it was also the case in the commemoration of our common friend, LAJOS VARGA, in the rich scientific production, between three periods.

The first period began when in 1905 he was appointed demonstrator of the Institute of General Zoology and Comparative Anatomy in the University of Kolozsvár, and it lasted up to 1924 when he received the Chair of the University of Szeged. This period started with two prize papers in which he described the animal species found in the vicinity of Kolozsvár. It was continued by describing the already mentioned turbellarian, named *Olisthanella hungarica,* this being Gelei's doctoral thesis. When he was the professor's assistant, he began his histological investigations into *Dendrocoelum lacteum,* the results of which were published in a monograph entitled „Tanulmányok a *Dendrocoelum lacteum* OERST. szövettanáról" (Studies in the histology of *Dendrocoelum lacteum* OERST.), for which the „Vitéz"-prize

of the Hungarian Academy of Sciences was awarded to him. The only defect of this work was that it was not published in any international language. He who knows that life — with its unextricable complexity, I could also say, mysterious character — becomes only cognizable in its phenomena and causes in the tissues and cells, presented to him as if by magic with an adequate technique: finds a revelation in almost any chapter of this valuable work. The beautiful illustrations, praising the artistic execution of the author's hand, the sober but clear interpretation of the relations seen under the lens of the microscope, the rich literary knowledge; all support the conclusion that the author of the work dealt with an inimitable ability and technique, and material which was more suitable for dissecting cytological problems than any other which could be found.

There falls to this time Gelei's other work, entitled „A kromoszómák hosszanti párosodása s a folyamat örökléstani jelentősége" (Longitudinal mating of chromosomes and the genetic importance of this process), being similarly of major significance and published by the Hungarian Academy of Sciences in 1920.

The promptings to this work were given to him by BOVERI in Würzburg who, as an experimentator, was respected by him as a second master. In the work, which is a pearl among the morphological cytological investigations, there was proved the genetically important fact that the chromosomes of the leptotene-stage thread mate longitudinally. By this process, as the authour himself writes, "the sticking together of two homologous chromosomes of paternal and maternal origins are meant, starting from their ends, while always qualitatively equal parts of these face each other". It is at the same time, made possible by this "mating" — the author continues — that, „in the way of the division of ripening, the number of chromosomes comes down to half, and previously that, while mating, the identical parts are exchanged and chromosomes of a new reconstruction created". In these theses — as GELEI himself says — there was established nothing new. It had already been pronounced by MONTGOMERI that the mating partners descended from two parents. SUTTAN declared the equivalence of their homology and SCHREINER *et al.* that of the parts facing one another in the pairs. All these were however, according to GELEI, but declarations which generally long preceded the evidence. His investigations, he says, "do mean a progress in as much as they prove the statements of the authors mentioned" and his own "identical opinion, every-where with direct observations".

For the investigations he used the ovary of the milk-white flatworm *(Dendrocoelum lacteum)*. He studied the oocytes and chromosomes in pulped and stained preparations. The examination with shredding suggested by FLEMMING in 1887 for cytological investigations, is — as GELEI says — comfortable but the results are only to be accepted "with due criticims and after the assessment of results on sections". To be sure, the process is very useful because in the preparations obtained in this way the cells are placed in a single layer and thus, touching the fixing solutions or their vapours immediately, are excellently fixed. The procedure is also good because the pulped preparations are investigated without being embedded and so the stains applied to the chromosomes exert a stronger effect on them than on sections made from an embedded substance. It is a particular advantage of these preparations that in them the nucleus can be seen in full while in sections, even if these are made in series, the connections are only to be found with great difficulty. GELEI made pulped preparations from his material, *Dendrocoelum lacteum* in the following way. Small pieces cut from the ovary were put on the slide and moved about with a dissec-

ting needle. The result was that the oocytes fell out of the ovary-piece and adhered to the slide. As in the oocytes of *Dendrocoelum* the nucleus is surrounded by the cytoplasm only in the form of a pale border, the resulting oocytes proved to be particularly suitable for investigation into the nuclear content. It was also easy recognize and study the constituents of nucleus and the chromosomes themselves in the preparations because the achromatin framing between the chromosomes remained colourless after staining. Because of this, the preparations were very good for investigating the chromosomes appearing in the oocytes. Some difficulty was, caused by the fact that only those chromosomes became sharply visible which were situated in the upper part of the preparation, looking towards the lens of the microscope. These obscure the chromosomes lying below them, making it very difficult to recognize, and still more to examine the latter. GELEI however, quickly and easly got round this problem. Instead of the usual slide he used a large gloss cover-ship and covered the preparation with similar cover-ship. In this way, he could examine both sides of the same oocytes. Another trouble that strongly impeded the investigations, was that the cell-saps evaporated in the dry air leaving an artefact unfit for use. Then came forward JÓZSEF GELEI, the microtechnicist, constructing a so-called dressing case for solving the task. In this he could produce preparations in a quantity according his choice in the presence of water-saturated air. The device was a square metal case the airspace of which could be cut off from the external dry air during pulping. The air filling the interior of the case could be preserved in a durably wet state with slips of wet paper. He could thus carry out fixing, as well.

He found Altman's fluid to be the most suitable for fixing the nuclear substance and the thread-chromosomes. A disadvantage of this was that he couldn't subsequently carry out any elective staining Flemming's fluid led in his hands to a good result, as modified according to BENDA, and with Apáthy's sublimated osmic acid mixture and his own formalin-osmium mixture. For staining, the procedure of ROMANOVSKY-GIEMSA was exclusively used, stainig the chromatinic substance in any form of it reddish violet. The colour did not become diffuse even when greatly magnified and in the preparation even the deepest lying details could be seen well. For making sections, the substance was fixed in one of the above mentioned fluids, and embedded in Apáthy's celloidin paraffin. From this, 1 to 5μ section series were made.

After using the procedures and methods enumerated, carefully, as new results for the science, the following were ascertained. When the oocytes achieved the size of motheroogonia, in the nucleus a separate glomus is formed of chromatic threads. The threads very likely correspond to the diploid 14 chromosome number. From the thread-glomus, as directed by the chromosomes, a form of bunch develops in the formation of which the leading part belongs to the centrosome. The chromosome number is still 14 in the bunch.

The thread-chromosomes, which show a regular granularity because of chromidia, are approximately as long as the chromosomes of oogonia. In the bunch, the double chromosome stock and the equal length of pairs can be established. The equally long, i. e. homologous chromosomes do not lie adjacently. The longitudinal mating occurs in the following way. The mating chromosome-ends come into close proximity to each other in a confined field. In this location, the "legs" of the chromosomes obtain a more or less parallel situation. In this situation between the chromosomes pointing into the same direction, some free ways suitable for moving come

into being. Then mating begins in the following way. The separate pairs contact each other as is to be explained by the appearance of the pairing instinct. Mating starts from the ends and continues towards the middle. In the meantime, the chromidia of the pairs set themselves face to face with one another in pairs. The adjacent pairs adhere to one another, are pressed together and grow shorter. The mating pairs, after mutually, exchanging their parts, are rearranged.

In the course of analysing the single phases of mating exactly, it became ascertained that chromosomes must have some facility of movement and displacement and, some thing consistent with this purpose is needed in their substance. As the free "legs" of the hardly adhered pairs are always of the same length, and in addition, the pairs are supplied with the equal number of chromidia and are equally thick, it can be considered as demonstrated that only the thread-chromosomes of equal length can be paired. With this, there was demonstrated, for *Dendrocoelum*, Montgomery's supposition that in every chromosome-pair a paternal and a maternal chromosome stick together. In respect of *Dendrocoelum*, the correctness of Suttan's supposition was also proved; that the two by two equally long chromosomes are homologous, and qualitatively equal but the chromosomes of different length are qualitatively different. On the basis of profound observations and the logical reasonings connected to them, Gelei's a final conclusion is that "like any mating cells or protozoa, chromosomes also get a new individuality during their rearrangement connected with their mating, as a consequence of which they do not transmit by heredity the same faculties which passed to them from their forbears".

I dont know what is said to all, this by the electron microscope, nucleic acids, gene-surgery, gene-transplantation, molecular biology and generally by the science of our age distributing many and great novelties, by the genetics, but I do know that József Gelei's analytical results concerning the longitudinal mating of chromosomes belong to the most beautiful achievements of experimental cytology. The questions that were answered by these brought us nearer to recognizing the laws of nature which are everywhere and always the same, unchanged and unchangeable.

The demonstration of the longitudinal mating of chromosomes was the outstanding result that assured GELEI a lasting name in experimental cytology. His durable demonstrations and fine drawings soon found their way into world literature and won high appreciation and honour not only for GELEI but to the Hungarian biological sciences, in general.

The second period of József Gelei's scientific reserach work began in 1925 and lasted until 1945. In this period he continued his histological and cytological research work concerning Turbellaria and described new flatworm species from the fauna of this country. He often visited the Biological Research Institute at Tihany and became intensively connected with the research work concerning the living world of Lake Balaton. In this period he began his investigations into Protozoa which led to world-wide success and raised him the ranks of the greatest protistologists of the world. Here were manifested his extraordinary many-sidedness and his comprehensive mind embracing the whole domain of general biology, comprising all of the provinces of systematics, ecology, ethology, physiology, and phylogenetics.

He was led by his general biological contemplation to the world of Protozoa where he, in this second period of his scientific activity, achieved so many successes and made so many valuable contributions.

The event starting these investigations of GELEI, as I learned from GELEI him-

self, was the following. As the newly appointed professor of zoology in Szeged, he visited a zoological morphological practical class led by BÉLA FARKAS, a later professor systematic zoology (zoological taxonomy) at the University of Szeged. In this practical training, the undergraduates examined *Paramaecia* collected in the borrowing pits at Szatymaz. GELEI sat down at the microscope of one of the undergraduates, and began to look at the *Paramaecia*. He was long staring at them because he had perceived already, at the first glance, that the animal was not the *Paramaecium caudatum* but another protozoan belonging to the Ciliates (Ciliata). This recognition turned Gelei's attention to the Ciliates living in the neighbourhood of Szeged and later to those living around the whole country. The high degree of organization by which these animals are characterized incited this biologist who was well versed in research into fine structures, to progress from looking for habitats and describing the species found, more and more towards investigating the internal organization. From among the results achieved in this respect, the demonstration of the neuronema systems and the description of the excretory organ systems is most considerable.

Neuronemata are called by GELEI the fine silvery lines demonstrated in the body of *Paramaecium caudatum* with his own silverizing procedure. He distinguished two parts of the neuronema systems being in contiguity with each other, attributing a function to these systems which is similar to that of the multicellular nervous system. One of these parts is called by him a central and the other a peripheral neuronema system. It is interesting that while concerning the neuron-linkages of Metazoa he professed — relying on the instructions of his master, APÁTHY — the tenet of continuity, in the neuronema system of Protozoa he demonstrated contiguity in the connection between central and peripheral systems. Gelei's establishments in regard to the neuronema systems have attracted great attention and found high appreciation in many places, together with similar results of KLEIN in Vienna. There were, of course, abundant difficulties, although those who had dealt with the physiology of Protozoa, and primarily of Ciliates, were fully aware of the fact of intracytoplasmic impulse conduction and supposed the presence of the element, of this conduction. This was not the case with the neurohistologists and among these MIHÁLY LENHOSSÉK who, as I heard from GELEI himself, was not inclined to consider the silvery lines made visible by impregnation, as neuro-elemets even after the conclusive activity of GELEI and his school for as many as ten years.

We have also confirmed that the silvery-line system is demonstrable with silver impregnation in the body of Holotricha infusoria, mainly of *Paramaecium caudatum*, but not the suggestion that the movement of Ciliates is governed by this. To be sure, when stained and impregnated the immense quantity of nerve fibres in the palatal mucosa of frogs, without having found the connections, I was almost convinced — and said so to GELEI — that the movement of cilia was directed by the nervous system. I had to entrust the solution of this problem to the electron microscope. I am unaware of the result in case of Ciliates, whether or not there was achieved anything new by means of the electron microscope. But I have become satisfied that in the case of Vertebrates it has not demonstrated any connection between cilia and the nervous system. I have carefully investigated the situation, in convincing photographs, in kidney and tongue of the frog where there are extremely imposing ciliary fields without finding, however, any connection between the nervous system and cilia.

Gelei's investigations, published concerning structure and function of the excretory organs of Protozoa, are neat and valuable. According to these, the excretory

organ of the higher Protozoa is the pulsating vacuole or, as named by GELEI, the throbbing small cavity, and the ducts leading there. All of these are preformed formations, having a definite place in the organism of the animal. There are two efferent ducts to discharge the products of decomposition. These are short tubes lined with ectoplasm, and surrounded by a thick cuticular ring. The efferent ducts are bordered towards the vesicle by a protoplasmatic valve. The efferent ducts are also standing formations, not disappearing on contraction (systole), only some parts of the wall come closer to one another, of the ducts leading there the content only became known after impregnation by silver and staining with osmic acid. The afferent ducts grow wider immediately before the vesicle to form ampoules connected to the vesicle by the spray duct. This clear and valuable work, giving a detailed description of the problem-complex, was published in Budapest, and entitled "A véglények kiválasztó szerve alkati, fejlődéstani és élettani szempontból" (The excretory organ of Protozoa from constitutional, evolutionary and physiological points of view), in 1935.

The third — and shortest — period of the scientific activity of JÓZSEF GELEI began in 1945 and lasted up to his death. In this time he continued collecting diligently, examined the material collected very thoroughly and published particularly his results which were valuable from the general biological point of view, in this country and abroad. He discovered mass productions and biocoenoses in the pools left behind after rainfalls and with the series of observations made there, he also came over to the meteorological biology. He was very much interested in this, as in everything he considered as new in biology. He diligently visited the springs and brooks in Bükk and Börzsöny, and looked for the interconnections between the living world, the situation, the seasons, and the weather. In 1950 his paper entitled "Az egysejtűek morphogenezise, tekintettel SEVERCOV morphogenetikus alapelveire" (Morphogenesis of Protozoa with regard to Severcov's morphogenetic basic principles). In this he found the thirteen basic principles applied by SEVERCOV, the prominent comparative anatomist, to demonstrating the origin of Metazoa, to be conclusive also in investigating the phylogeny of Protozoa. In this connection, he himself laid down four more basic principles considered as serviceable for demonstration in the phylogeny of both Protozoa and Metazoa. By this time he already felt and knew that, as he said to me, "his heart is limping".

The slowly but surely killing disease progressed from day to day. He nonetheless worked and, although he was histologist he hoped in secret. His last way, leading him to the mountain of Dobogókő, finished in a cilinic of the University Medical School in Budapest. Here stopped the motor because the brooklet "which is driving the heart", ceased flowing.

I have drawn the life of a man as I have seen as y have heard and as y have read it in a maze of writings. It is already 25 years since József GELEI left us. His mortal remains merged into the sweet mother earth but the chromosomes he took along as an inheritance from the river Olt to the riverside of the Tisza, are surviving, moving, looking for place, mating longitudially, and the thread of life is more elongated by the MOIRAI. His memory is still alive in his numerous family, each member of which was loved by him very much. It is preserved by the forests, the fields, the talkative springs, and by Mother Nature whose heart-beat he so frequently listened to with such an unextinguishable love. It is preserved by us, Hungarian biologists, by the immense host of biologists all over the world, by his works of imperishable value

in which he bequeathed to us the products of his winged spirit and artistic hand, furnishing evidence that he loved science passionately, could be enthusiastic about it, could work, struggle and, if necessary, suffer for it.

Prof. Dr. A. ÁBRAHÁM

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TEN YEARS OF THE DEPARTMENT OF COMPARATIVE PHYSIOLOGY

In 1966 the board of leaders of our University adopted a resolution according to which the zoological departments of the Faculty of Natural Sciences were to be reorganized for the sake of modernization of the educational and research activities. Animal Physiology (or by its present name: Comparative Physiology) had been taught at the Department of General Zoology and Biology (headed by Academician AMBRUS ÁBRAHÁM) by FERENC BICZÓK Ph. D., among other zoological disciplines, without separate teaching and research staff. After the retirement of Professor ÁBRAHÁM the anatomy, histology and embryology staff moved to the Department of Systematic Zoology (headed by Academician GÁBOR KOLOZSVÁRY). At the same time a Dapartment of Animal Physiology was established. According to a decree of the Ministry of Cultural Affairs, the existence of the Department can be counted

The new Biology Building of the Attila József University giving accomodation for the Departments of Genetics, Biochemistry, Microbiology and Comparative Physiology since 1974.

officially from the lst of November 1967. The direction of the Department was taken over by OTTÓ FEHÉR M. D., who was previously a university lecturer at the Department of Physiology of the Medical School in Debrecen. Thus, with the generous help of Academician Prof. FERENC MÁRTA, Rector of the University, Academician GYULA GRASSELLY, Dean of the Faculty, Prof. IMRE HORVÁTH Ph. D., President of the Biological Section, and FERENC HERCEG, Bursar of the University, teaching and research activities in comparative physiology could be started. At the same time far-reaching work commenced for the creation of the material and personal conditions of a full-valued university institution. The laboratories had to be reconstructed

for the aims of physiological work; a room for laboratory animals was built and there was an urgent need for modern physiological apparatus for teaching and research. Academician KÁROLY POLINSZKY, the Deputy Minister, kindly placed at our disposal a considerable sum in foreign currency which allowed us to furnish the first neurophysiological laboratory. In the preparatory, organizational and technical work an outstanding role was played by GÉZA TURY Ph. D., one of the founders of the Department. In starting the teaching and research activities, LAJOS ERDÉLYI Ph. D. gave indispensable help. This group of founders was later joined GÁBOR BÁLINT M. D. (1969—1970), MAGDOLNA SZENTE Ph. D. (1970—), ISTVÁN PÓR Ph. D. (1971—1975), IMRE GAÁL Ph. D. (1973—1978), ATTILA BARANYI Ph. D. (1975—) FERENC PONGRÁCZ (1975—), and JÓZSEF TOLDI (1976—).

At that time the technical staff consisted of GÉZA MRÁZ, ERZSÉBET DÁNOS and SÁNDOR MOTZWICKLER. Mrs. Anna Basch was the Department's secretary. The Electron Microscope Laboratory functioned as a part of the Department from 1965, headed initially by Prof. BERTALAN CSILLIK M. D. and later by FERENC JOÓ M. D. The scientific staff consisted of NORBERT HALÁSZ Ph. D. and ÁRPÁD PÁRDUCZ Ph. D. The laboratory was supported by the Hungarian Academy of Sciences. Since 1972 the Laboratory has continued its work as the Group of Molecular Neurobiology in the Biological Research Center of the Academy in Szeged.

In 1973 a new Electron Microscope Laboratory was established to aid the scientific research in the Faculty. Members of the scientific staff are: IMRE ROJIK Ph. D. and IMRE HORVÁTH Ph. D., with the technical assistance of Mrs. ZSUZSA FEJES. The Laboratory is managed by the Director of the Department.

In 1967 a Group of Genetics was also organized within the body of the Department. Under the leadership of LAJOS ALFÖLDI M. D., Mrs. MÁRIA HORVÁTH (1968—1974) and IMRE ROJIK (1967—1973) carried out scientific and educational activity until 1974.

In 1970 a Group of Biochemistry was founded under the leadership of BÉLA MATKOVICS Ph. D., M. D.; from 1972 it was united with the Group of Genetics and functioned as a separate unit in the body of the Department until 1974.

Form the beginning the Department gave place and other facilities for the work of the biologist-didactician LÁSZLÓ KÖRTVÉLYESSY Ph. D., who until his retirement in 1977 carried out succesful educational and scientific activity.

The range of the educational tasks covered by the Department is rather wide. Teacher-students in biology-chemistry, and students in biology attend lectures and practical lessons in comparative physiology in the Department. Lectures in school-hygiene and animal husbandry are also delivered by members of the Department. As mentioned above, education in biological didactics was taught here for ten years.

Training in comparative physiology at the university level does not have a long past in Hungary (Prof. GYÖRGY ÁDÁM M. D. 1965), and thus one of the most urgent tasks was the definition and standardization of the subject matter of the lectures and practical lessons. As a first step, a guide book was published by OTTO FEHÉR, LAJOS ERDÉLYI, JÓZSEF FAISZT, GÁBOR HOLLÓSI and MIHÁLY KURCZ, with the title "Exercises and Experimental Demonstrations in Comparative Physiology".

In 1975 Academician GYÖRGY ÁDÁM M. D. and Prof. OTTÓ FEHÉR M. D. published the Textbook "Coomparative Physiology". The book was rewarded with a "Niveau Prize" by the Ministry of Education in 1977.

Meanwhile a modern program has been developed in the student laboratory

exercises, supported by instrumentation of a high level. Methods have been elaborated for checking the proficiency of the students during the semesters. As an important branch of the educational activity 26 students were instructed in preparing their diploma-work and 8 theses were submitted for Ph. D. degree by scientific co-workers of the Department.

Thus comparative physiology has gained its proper place in our University as an important discipline in education and scientific research.

The main objective of the scientific investigations in the Department has been the nervous system. This was fairly natural, because the founders (FEHÉR, TURY, ERDÉLYI) has done considerable work in neurobiology up to that time. From 1967 a complex neurobiological research group was built up and set into motion, which exerts its activity in the following main directions:

a) The origin of cortical evoked and seizure potentials. Computer modelling of neuronal nets producing them (SZENTE, PÓR, PONGRÁCZ).
b) Plasticity of cerebral cortical functions (BARANYI, TOLDI).
c) Nervous processes in the Molluscan heart and nervous system (ERDÉLYI).
d) Complex morpho-physiological examination of cerebral synaptic transmission (JOÓ, PÁRDUCZ, HALÁSZ in collaboration).
e) Morphological-biochemical examination of cortical excitatory processes (ROJIK, GAÁL).
f) Study of the spreading depression (TURY).

The study of the spreading depression has been finished. Theme *e)* is financed as part of the central research plan: "Investigation of biologically-active compounds".

The members of the staff have read 53 lectures at national and 11 lecturs at international congresses and symposia, and published 40 full-length papers. The leader of the Department wrote his academic dissertation mainly on the basis of experiments performed in Szeged, and was declared a "Doctor of Medical Sciences" in 1973. Further scientific qualifications are in preparation. The collaborative work of the Department with the Electron Microscope Laboratory and Cybernatics Laboratory was awarded an academic prize in 1972. Prof. OTTÓ FEHÉR M. D. was rewarded with a shared academic prize for his scientific work in 1977.

The repertoire of scientific research methods applied by the Department has become rather wide and is of an interdisciplinary character. The most important methods are as follows: stimulation and recording in any part of the central and peripheral nervous system with macroelectrodes; electroencephalography; stereotaxic techniques; intracellular recording and stimulation, polarization, and conductance measurement; the voltage clamp method (under development); extracellular microelectrode techniques; microiontophoresis, examination and averaging of evoked cortical potentials; standard methods for examination of the heart, blood circulation, breathing and metabolic rate; tissue fractionation with density gradient centrifugation; polyacrylamide gel electrophoresis; gel chromatography; standard electronmicroscopic methods; light- and electronmicroscopic autoradiography; etc.

The electrical engineer of the Department (FERENC PONGRÁCZ) has constructed equipment for intracellular recording, polarization and conductance measurement. The computer modelling of nervous processes has commenced, too.

As regards the production of the mechanical workshop, several instruments are worthy of emphasis: a middle-school kymographion (SÁNDOR MOTZWICKLER),

a thermo-stabilizer for animal experiments and a regulated current source for the student exercises (PÉTER TRÁM).

The scientific equipping of the Department commenced in 1969, when high-quality amplifiers, stimulators, oscilloscopes and other apparatus were placed at our disposal for research and teaching. Now four wellequipped physiological, a chemical and a morphological laboratory serve as the basis for progress in neurobiology and education.

In 1974 the Department and the Electron Microscope Laboratory moved to the new biological building of the University and were generously accommodated in more than 900 square metres.

The whole staff of the Department is doing its best to use all the facilities afforded by the Socialist State in order to educate the new intelligentsia and to elaborate a deeper knowledge of the nervous system.

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ULTRASTRUCTURE INVESTIGATIONS INTO FOSSIL SALVINIACEAE SPORES

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Abstract

In this paper the results of the transmission electron microscopical examinations of an upper Cretaceous Salviniaceae sporangium fraction are summarized. The ultrastructure of the general enough spongious intermediary substance is at first described, as recognized at the fossil Salviniaceae spores, in the course of the light-microscopical examinations. The submicroscopical structure of the spore-wall is identical with the "modern type" from the upper Cretaceous, lower Paleogene Period, viz. two layers on the spore-wall can only be distinguished on the basis of the electron affinity.

Introduction

The first data on the submicroscopical structure of the wall of the fossil spores were published by PETTITT (1966). Then KEDVES and PÁRDUTZ (1973) established on Schizaeaceae and Gleicheniaceae spores from the upper Cretaceous and lower Tertiary Periods that the two layers (ectexosporium, resp. endexosporium) can only be isolated on the basis of electron affinity. The spore-walls of this Period significantly differ in respect of ultrastructure from those of the Palaeozoic Era and in point of building up they are simpler. KEMPF (1969 a, b, 1971) investigated into the submicroscopical structure of the micro and megaspore-walls of the fossil *Azolla* and *Salvinia*. He established about the structure of the perine (1969a) that the tectum, the columella layer, and the foot layer are similar in their arrangement to the sporodermis of Angiospermae. The detail of the wall below the perine, the ectexosporium in these spores agrees essentially with the type observed by us, as well.

Materials and Methods

In the course of our investigations into the ultrastructure of the fossil spore-pollen exine, we found in one of the blocks embedded forms from the upper Cretaceous sediments of the Farafra oasis, a sporangium fraction of which, with a light microscope, the fgen. of Hydrosporis can be recognized. The detailed description of the method of this investigation is to be found in the paper of KEDVES and PÁRDUTZ (1970).

Plate 1

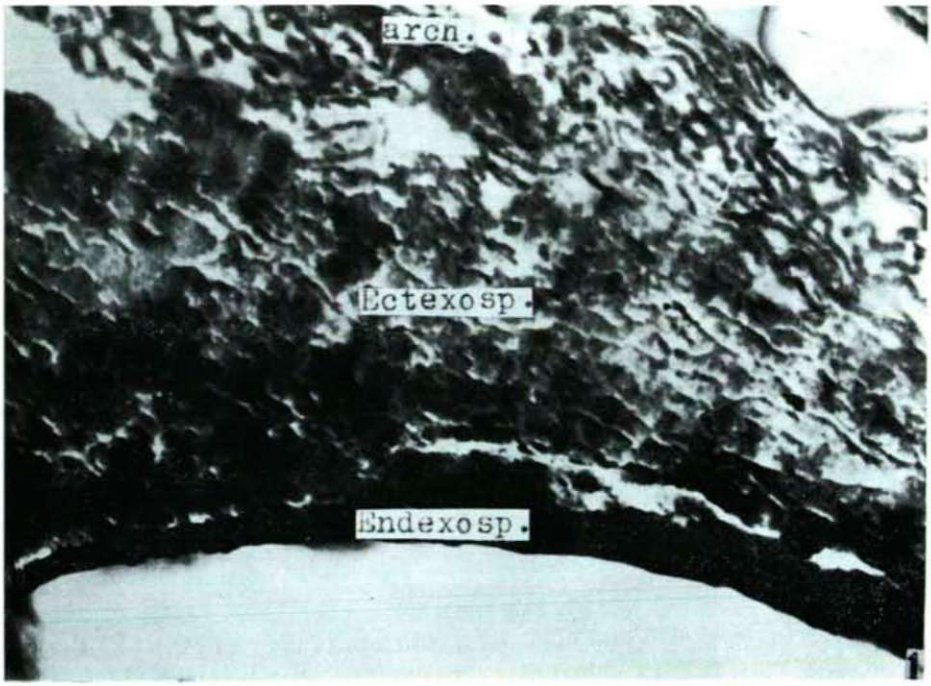
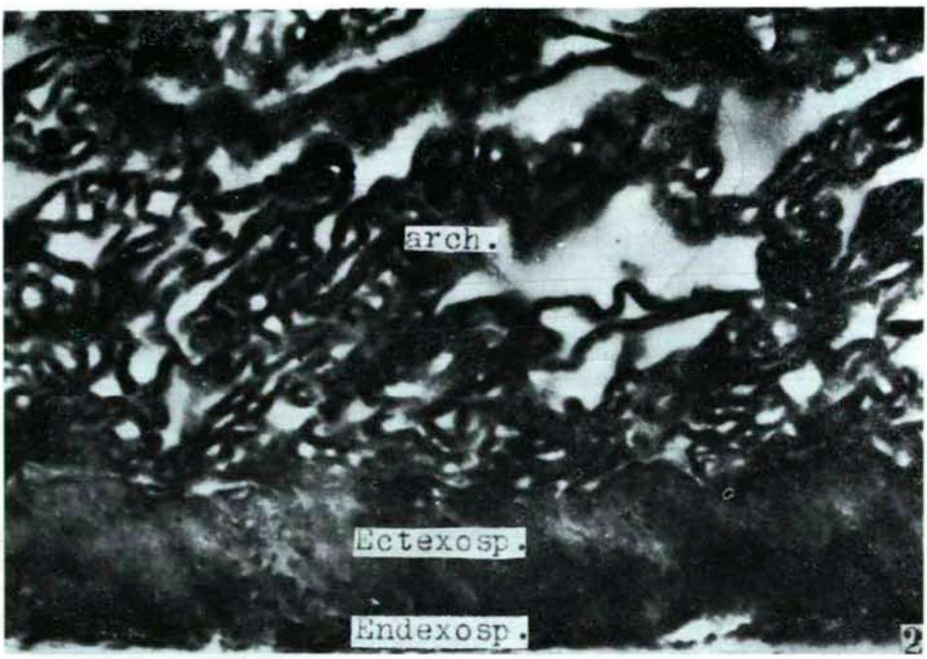


Plate 2



Results

The intermediary substance surrounding the spores being probably the remainder of the archesporium, is mostly of lamellar ultrastructure (Plate 1, 2). Between the lamellae there are sporadically in our crossectional picture also some tiny submicroscopical formations, with an elliptical shape.

In respect of the ultrastructure of the spore-wall, we could establish two types: In case of the first type the external part of the wall is in a very close connection with the lamellar part of the archesporiumwall. The transition between archesporium and ectexosporium is often almost continuous. This is the cause of that the sectional picture of the ornamental elements of the surface cannot be observed at this type. The ectexosporium is of expressly lamellar structure, the single lamellae are much thicker than the lamellae of the intermediary substance and very often anastomose. The endexosporium is of very strong electron affinity, homogeneous, in this case, the difference between ectexosporium and endexosporium is very express (Plate 1).

At the other type, in the external part of the spore wall, the sectional picture of the surface ornamental elements is to be observed well. The surface is uneven, there are protrusions on it, the decoration is probably granular. The surface of the ectexosporium is well-isolated from the lamellae of the archesporium. As to its substance, as opposed to the former type, it is homogeneous. The electron affinity of the endexosporium is of much lower degree in this case than at the former type. In this case, even the section of the laesura of the tetrad mark was successful. This is a narrow cleavage covered by the outermost layer of the ectexosporium.

Discussion

POTONIÉ (1962) was writing in his monograph, written on the light-microscopical structure of the associated sporomorphs at the Salviniaceae, about an intermediary substance of spongy structure at Palaeozoic forms, as well. On the one hand, he establishes that microchemically this is similar to the sporopollenin, on the other hand, that it does not belong to the structure of exine. This establishment is supported by our ultrastructure investigations, added anyway that, in case of this intermediary substance, the question in point may have been the archesporium, namely a well fossilized part of that. As to the ultrastructure of the wall of spores, it essentially agrees with the earlier recognized "modern type" which is homogeneous, without any articulation. The endexosporium only differs from the ectexosporium exclusively by its electron affinity. On the basis of the foregoing results from a younger age we must accept the result that, in case of the modern fossil Pteridophyte spores, the ultrastructure is not differencing value, in contradiction to those described from the Palaeozoic Era where more than one type can be separated. This may have followed from that the undifferentiated fern taxa of the Palaeozoic Era have produced more types also in respect of ultrastructure than the already differentiated forms from a younger age. As regards the two types to be established in the ultrastructure of the spore wall, we may first of all think on that the maturity state of the spores occurring in the massula is different, namely in case when the connection between the remains of ectexosporium and archesporium is very close that is representing a more immature state as opposed to the well-differentiated spore wall.

Hydrosporis fsp.

Plate 1. — A detail of the spore wall. The lamellar ultrastructure of the ectexosporium is express. M: ×25.000

Plate 2. — Ectexosporium of homogeneous ultrastructure. M: ×25.000

arch. = archesporium
Ectexosp. = ectexosporium
Endexosp. = endexosporium

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PALYNOLOGICAL INVESTIGATIONS INTO SEDIMENTS OF THE LOWER PALAEOGENE PERIOD IN BULGARIA

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Abstract

We have performed spore-pollen investigations into the sediments of the lower Palaeogene Period in Pleven. The sporomorphous assemblages are extremely rich in Hystrichosphaeridae remains, and a part of the samples examined in sporomorphs, as well. The Pteridophyta are represented by 10, the Gymnospermatophyta by 2, the Angiospermatophyta by 39 microremains. At the marl-level in Bozurica the pine-pollen grains with bladders predominate, and, apart from these, the quantity of the forms of Castanea type is considerable. In the spore-pollen assemblage of the habitat of Komarevo the dominance of the pollen grains referring to the genus Castanea is prominent. The qualitative composition of the samples investigated points to the lower Eocene Period (lower Sparnacian Stage).

Introduction

The sporomorphs of the lower Tertiary sediments in Bulgaria were treated of by ČERNJAVSKA (1966, 1967a, b, 1969, 1970a, b, 1973) and ČERNJAVSKA and PETKOVA (1968). Their investigations included the upper Eocene, resp. the Oligocene sediments. In connection with the upper Eocene vegetation it was established that although it was very similar to the German upper Eocene, nevertheless there could be ascertained some differences due to the territorial origin. In connection with the Eocene spore-pollen assemblages in Hungary it also arose that they differ from the West-European sediments, primarily from the types well known from the classical sediments of the Parisian basin in more, not unimportant characteristics. This is particularly obvious first of all at the pollen of angiosperms, and within this at the pollen grains of short axis. Owing to this, there was necessitated the description of several new form-species (KEDVES 1974). These results are raising the idea that the extremely definite regional differences which were ascertained in the angiospermous vegetation of the upper Cretaceous Period manifest themselves, though not in so high degree, even in the lower Tertiary Period. Apart from this, at any rate, it is possible, too, that the differences observed in the lower Tertiary may already be attributed to other causes than in the upper Cretaceous Period. In order to bring this problem forward, my interest turned to the sporomorphs of the sediments in the South-European lower Tertiary. Within this, from the point of view of the phylogeny of the angiosperms, one of the crucial periods, the Palaeocene one seemed to me very considerable. To my request, my colleague, S. ČERNJAVSKA, was good enough to place at my disposal several samples for investigation. The results of these are summed up in this work.

Materials and Methods

The samples investigated have been collected by Em. Belmoustakov. These are as follows: Pleven-1, Bozurica, marl level; Pleven-2, Bozurica; Pleven-3, Petrnica; Pleven-4, Komarevo — these are determined as originating from the Palaeocene Epoch. From the habitat at Lukovit the Lutetian Stage is represented by one sample. The exposure of sporomorphs took place with HCl, for precipitating $ZnCl_2$ was used, then a treatment with HF followed. The clearing of precipitation was carried out with borated hydrochloric acid. We permformed the investigation of sporomorphs with light-microscopic method, taking into consideration not only the qualitative but also the quantitative data of every sample. From among the microphotographs, there are only published those made of a new type which could not be determined nearer or of the form-species that differ from the typical forms to a certain extent.

Results

1. In the course of the investigations, we succeeded in demonstrating the following sporomorphous taxons:

Fgen.: *Leiotriletes* (NAUMOVA 1937) R. POT. et KR. 1954. *L. adriennis* (R. POT. et GELL. 1933) W. KR. 1959, Schizaeaceae, cf. *Lygodium, L. dorogensis* (KDS. 1960) KDS. 1961, Schizaeaceae, cf. *Lygodium.*

Fgen.: *Concavisporites* PF. 1953. C. *(Concavisporites) hungaricus* KDS. 1973, Gleicheniaceae.

Fgen.: *Trilites* COOKSON 1947 ex COUPER 1953. *T. paravallatus* W. KR. 1959, Schizaeaceae, *Lygodium* v. Dicksoniaceae, *Cibotium.*

Fgen.: *Ischyosporites* BALME 1957. *I. asolidus* (W. KR. 1959) W. KR. 1967, Schizaeaceae.

Fgen.: *Foveasporis* W. KR. 1959. F. cf. *linearis* W. KR. 1959 (Plate 1, 2). The specimens occurring in our material are somewhat smaller than the typical forms described from the middle Eocene in Geiseltal. Further on, the densennes of the foveae of the exosporium is also somewhat smaller.

Fgen.: *Polypodiaceoisporites* R. POT. 1956. *P. brevisculptatus* KDS. 1973, Pteridaceae, *P. verruspeciosus* W. KR. 1959, Pteridaceae, P. fsp. Pteridaceae (Plate 3, 4).

Fgen.: *Laevigatosporites* IBR. 1933. *L. haardti* (R. POT. et VEN. 1934) TH. et PF. 1953 subfsp. *hardtioides* W. KR. 1967, Polypodiaceae.

The recycled spores from the lower Cretaceous Period came to light from the *Appendicisporites* fgen. (Plate 5, 6).

Fgen.: *Pityosporites* SEWARD 1914. *P. labdacus* (R. POT. 1931b) TH. et PF. 1953 subfsp. *labdacus*, Abietaceae, *Pinus*, *P. microalatus* (R. POT. 1931b) TH. et PF. 1953, Abietaceae, *Pinus.*

Fgen.: *Trudopollis* PF. 1953. T. $fsp._1$, (Plate 7, 8). This type is also known from the Thanetian of Menat (KEDVES 1967, Pl. I, 12, 13), T. $fsp._2$ (Plate 9, 10).

Fgen.: *Interporopollenites* WEYL. et KRIEG. 1953. I. fsp. (Plate, 11, 12). This fgen. is represented by a specimen in a bad enough state of preservation.

Fgen.: *Interpollis* W. KR. 1961. *I. supplingensis* (PF. 1953) W. KR. 1961, *I. microsupplingensis* W. KR. 1961, *I. velum* W. KR. 1961.

Fgen.: *Nudopollis* PF. 1953. *N. minutus* ZAKL. 1963.

Fgen.: *Plicapollis* PF. 1953. *P. pseudoexcelsus* (W. KR. 1958) W. KR. 1961 subfsp. *turgidus* PF. 1953, Myricaceae.

Fgen.: *Basopollis* PF. 1953. B. fsp. (Plate, 13, 14).

Fgen.: *Triatriopollenites* Pf. 1953. T. cf. *podagrarius* (Gladkova 1965) Kds. 1974, Myricaceae, *T. sauerae* (Gladkova 1965) Kds. 1974, Myricaceae, *T. aroboratus* Pf. 1953, Myricaceae.

Fgen.: *Plicatopollis* W. Kr. 1962. *P. lunatus* Kds. 1974, Juglandaceae.

Fgen.: *Platycaryapollenites* E. Nagy 1969. P. $fsp._{1-2}$, Juglandaceae, *Platycarya* (Plate 15—18).

The detailed taxonomical elaboration of the Palaeogene types of the form-genus requires still further work.

Fgen.: *Triporopollenites* Pf. et Th. 1953. *T. balinkaense* Kds. 1974. subfsp. *balinkaense*, cf. Ulmaceae, *T. undulatus* Pf. 1953, Ulmaceae, *T. pflugi* Kds. 1974, Juglandaceae v. Ulmaceae, *T. spackmanii* (Traverse 1955) Kds. 1970, Corylaceae, *T. robustus* Pf. 1953. subfsp. *robustus*, cf. Betulaceae, *T. nointelensis* Kds. 1970, Corylaceae, *T. urkutensis* Kds. 1974, Juglandaceae v. Betulaceae, *T. constans* Takahashi 1961, Corylaceae.

Fgen.: *Subtriporopollenites* Pf. et Th. 1953. *S. urkutensis* Kds. 1974, Juglandaceae cf. *Carya, S. sympathicus* (Botscharnikova 1960) Kds. 1970, Juglandaceae, *S. constans* Pf. 1953 subfsp. *constans* Juglandaceae.

Fgen.: *Alnipollenites* R. Pot. 1934. *A. verus* (R. Pot. 1931a) R. Pot. 1934 f. *hoellingi* R. Pot. 1931b, Betulaceae, *Alnus*.

Fgen.: *Pentapollenites* W. Kr. 1962. *P. laevigatus* W. Kr. 1962 subfsp. *laevigatus* Elaeagnaceae v. Simarubaceae.

Fgen.: *Monocolpopollenites* Th. et Pf. 1953. *M. tranquillus* (R. Pot. 1934) Th. et Pf. 1953 subfsp. *tranquillus*, Palmae.

Fgen.: *Cupuliferoidaepollenites* R. Pot. 1960. *C. quisqualis* (R. Pot. 1934) R. Pot. 1960, Fagaceae v. Leguminosae, Cf. *C. liblarensis* (Thoms. in Pot., Thoms. et Thierg. 1950) R. Pot. 1960, Fagaceae v. Leguminosae.

Fgen.: *Cupuliferoipollenites* R. Pot. 1960 non 1951. *C. pusillus* (R. Pot. 1934) R. Pot. 1960, Fagaceae, cf. *Castanea, C. oviformis* (R. Pot. 1931a) R. Pot. 1960, Fagaceae, *Castanea*.

Fgen.: *Cyrillaceaepollenites* (Mürriger et Pflug 1951) R. Pot. 1960. *C. barghoorniacus* (Traverse 1955) R. Pot. 1960, Cyrillaceae, Clethraceae v. Theaceae.

Fgen.: *Pleurospermaepollenites* Kulkova 1973. P. fsp. ? Umbelliferae (Plate 19, 20).

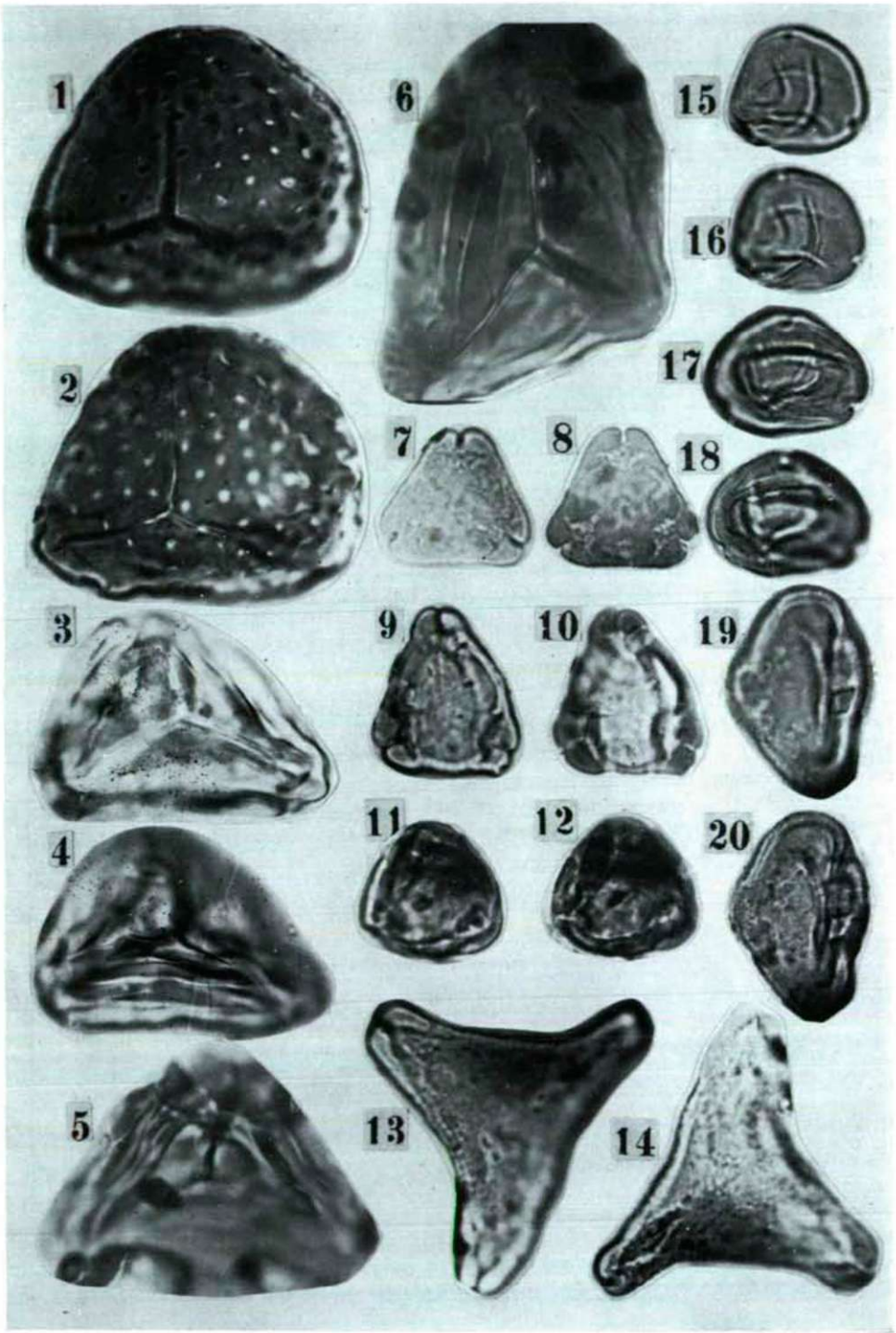
Fgen.: *Nyssapollenites* Thiergart 1937. *N. kruschi* (R. Pot. 1934) Simoncsics 1969 subfsp. *analepticus* (R. Pot. 1934) Simoncsics 1969, Nyssaceae.

Fgen.: *Ilexpollenites* (Thiergart 1937) R. Pot. 1960. *I. margaritatus* (R. Pot. 1931a) Thg. 1937 f. *medius* Pf. et Th. 1953, Aquifoliaceae. *Foveatricolporites* Pierce 1961. *F. gruas-cavagnettoae* Kds. 1977, cf. Rhamnaceae.

The spores and pollen grains refer to the following phylogenetical taxa:

Pteridophyta
Pteropsida (Schizaeaceae, cf. *Lygodium*, Dicksoniaceae, *Cibotium*, Gleicheniaceae, Pteridaceae, Polypodiaceae).
Gymnospermatophyta
Coniferopsida (Abietaceae, *Pinus*).
Angiospermatophyta
Dicotyledonopsida (Fabales, Elaeagnaceae, Nyssaceae, Simurubaceae, Aquifoliaceae; *Ilex*, cf. Rhamnaceae, Cyrillaceae, Clethraceae, ? Umbelliferae, Theaceae,

Plate 1



Ulmaceae, Betulaceae; *Alnus*, Corylaceae, Fagaceae; cf. *Castanea*, Juglandaceae, cf. *Carya*, Myricaceae.
Monocotyledonopsida (Palmae).

The quantitative data led to the following results:
Pleven

1. Bozurica (marl-level). It is comparatively poor in sporomorphs. The pollen of the pine with bladders and Fagaceae is relatively high. The sample contains a great number of Hystrichosphaeridae showing the saltwater environment.

2. Bozurica (?marl-level, Pleven—2). It is very rich in microfossils. Here similarly the pine with bladders and the Fagaceae pollen grains occur in a considerable amount. The number of Hystrichosphaeridae remains is extremely high.

3. Petrnica. Few sporomorphs with comparatively many Hystrichosphaeridae.

4. Komarevo — it is rich in micro-remains, the Fagaceae pollen grains predominate. There are similarly plenty of Hystrichosphaeridae. Lukovit (middle Eocene).
It does not contain quantitatively appreciable sporomorphs.

Discussion

The samples investigated on the basis of the demonstrated sporomorph-taxa cannot be considered as rich. None the less, on the basis of the high specimen number, certain conclusions may be drawn:

1. Stratigraphic conclusion

In the Lower Tertiary Period, as well, the angiospermous pollen grains have particular importance in respect of determining the geological age. The presence of Normapolles is, at any rate, referring to the older Tertiary. Thus the *Trudopollis* and *Interporopollenites* genera occur down to the lower Eocene but their main occurrence is the upper Cretaceous Period. The types of *Interpollis, Nudopollis, Plicapollis* (pseudoexcelsus), and *Basopollis* refer to the lower Eocene. From among the *Postnormapolles*, observed from the lower Eocene in Hungary, several common form-species occurred out of the *Triporopollenites* and *Subtriporopollenites*. It is essential that the typical pollen grains of the Palaeocene Epoch — *Stephanoporopollenites hexaradiatus* — are absent. The rather important types accompanying these pollen grains are similarly missing — like *Vacuopollis concavus, Nudopollis terminalis,*

◂ Plate 1

1,2. — *Foveasporis* cf. *linearis* W. Kr. 1959, Pleven 4/26; 17.7/113.2.
3,4. — *Polypodiaceoisporites* fsp., Pteridaceae, Pleven 4/9; 17.8/109.8.
5. — *Appendicisporites* fsp.$_1$, Pleven 2/26; 15.9/104.5.
6. — *Appendicisporites* fsp.$_2$, Pleven 2/27; 9.1/109.5.
7,8. — *Trudopollis* fsp.$_1$, Pleven 4/33; 7,2/106,2.
9,10. — *Trudopollis* fsp.$_2$, Pleven 4/27; 10.7/103.6.
11,12. — *Interporopollenites* fsp., Pleven 4/31; 15.0/108.3.
13,14. — *Basopollis* fsp., Pleven 4/30; 31.3/106.4.
15,16. — *Platycaryapollenites* fsp.$_1$, Juglandaceae, *Platycarya*, Pleven 4/7; 19.6/114.3.
17,18. — *Platycaryapollenites* fsp.$_2$, Juglandaceae, *Platycarya*, Pleven 4/20; 15.1/112.8.
19,20. — *Pleurospermaepollenites* fsp., ?Umbelliferae, Pleven 4/22; 14.8/106.7.
N: ×1000

N. endangulatus. The geological age of the samples investigated is therefore to be fixed on the lower Eocene. Taking into consideration the main types of the Paris Basin, we have reckon primarily with the lower Sparnacian Stage, owing to the older *Normapolles* pollen grains. On the other hand, one part of the older *Postnormapolles* accompanying these are missing. It is a difference too, that the ancient Myricaceae *(Plicapollis)* and Juglandaceae *(Platycaryapollenites, Plicatopollis)* are represented but in the slightest degree in the assemblages. Because of this and of the connection with the lower Eocene in Hungary, we must come to the result Cernjavska's establishment (1967a, 1970a) concerning the upper Eocene holds also true in respect of the lower Eocene. According to this, the Eocene vegetation in Bulgaria differentiates in its details from the Central — and West-European ones. It is to be mentioned as an interesting characteristic that the pollen grain of the *Alnus* genus occurred. This appears namely mainly in the upper Eocene in considerable quantities and is represented here only in the upper Oligocene.

2. Palaeobotanical conclusions

The representants of Pteridophyta are, by far the greatest number, of tropical character. It is interesting, although a far-reaching conclusion cannot be drawn from it, that the spores of the *Anemia* genus have not occurred in our material. Two types of the Abietaceae *Pinus* genus correspond to the general character of the lower Eocene floras but the comparatively high amount rather begins in the upper Eocene. The lack of the pollen grains of Taxodiaceae-Cupressaceae is interesting and unaccustomed. A considerable part of Dicotyledonopsida are represented by the amentiferous plants. On the basis of richness in form and number, these are most important. The great number of the pollen grains of *Castanea* type refers to a semiterrestrial bog. Another bog assemblage cannot be concluded from these. In higher areas *Pinus* forests may have been. In this case, however, we have, to refer to that the pollen production of pines is high and that they are transported far. Their quantitative data are, therefore, to be observed with criticism.

It is uncommon, as well, as compared with the lower Eocene floras, that the Myricaceae bog could not be demonstrated. It is similarly remarkable that the occurrence of the pollen grains of Palmae is extremely restrained.

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THE EFFECT OF COVERING WITH A TRANSPARENT PLASTIC SHEET, ON THE TISSUE STRUCTURE OF THE LEAVES OF BEAN PLANTS

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Abstract

Field experiments demonstrated that covering plants with colourless and orange plastic sheets resulted in considerable increases in the dry weight of shoots, and the crop, and changes in the tissue structure of the leaves. There is a close connection between the ratio of spongy parenchyma and the dry weight of shoot. As a consequence of being covered, the cells of the palisade parenchyma became nearly isodiametrical, the number of stomata and the thickness of epidermis are reduced. Underneath the orange sheet, the amphistomatic leaves became almost hypostomatic.

Introduction

Among the plant tissues, the structure of the assimilating parenchyma of the leaf and that of the epidermis are the most influenced by light. The effect of light is considerable because there is a close relationship between the tissue structure of the leaf and the organic-matter production.

It was established by HESSELMANN, as early as 1904, that the leaves of southern exposure of a shrub *Corylus avellana* L., developed under natural conditions, were thick, with a double layer of palisade parenchyma. Inside the shrub, where the intensity of illumination was ten times lower, leaves were much thinner, and the palisade parenchyma consists of a single layer of cells.

It was demonstrated by us, too, in our earlier investigations (PATAKY, 1969), that within the foliage of *Salix alba* L., there are significant changes in the tissue structure of the leaves as a result of changing light conditions.

There are several other reports demonstrating that the tissue structure of the leaf is generally related to the intensity of illumination, from ferns up to the flowering plants:

GRAHL & WILD (1973) observed two different phenotypes of *Sinapis alba* L., as a result of light intensity. Under intense light the plants developed a thick mesophyll with a stratified palisade parenchyma and a thinner spongy parenchyma.

A still more considerable change in the mesophyll of the leaf was observed by STARZECKI (1958). The mesophylls of the leaves of *Asplenium trichomanes* L. and *A. ruta-muraria* L., when grown in full sunshine, were well-developed and consisted of both palisade and spongy parenchymas. The leaves of plants, living in a cave, 20 m from the entrance, were thin and their mesophyll consisted only of spongy parenchyma.

TAKÁCS (1973), using *Lactuca sativa* L., *Spinacia oleracea* and *Rumex acetosa* L.,

established that, as a function of light intensity, leaves of different thickness developed and the proportions of palisade and spongy parenchymas changed. The structure of the epidermis is also influenced by light intensity. Shenikov's establishment (1953), according to which, reduction of the intensity of illumination results in enlargement of the epidermal cells, reduction in the number of stomata, shortening of the vascular system of the leaf, and the cell wall becoming more winding: is generally accepted.

In this paper, the effect exerted on the leaf-tissue structure by covering the plant with different nets of mesh, is investigated. Primarily, the structures of mesophyll and epidermis have been followed.

Materials and Methods

The investigations were performed using beans (*Phaseolus vulgaris L.* — a kind of dodder). Sowing took place on July 2, 1973, in the Botanical Garden of the Department of Botany, Attila József University, Szeged, in three repetitions, 2×3 m plots, in a random block arrangement. Row and stem distances were 30 cm.

Three plots were covered with colourless and three with orange plastic sheets. The plots remained covered from sowing until elaborating the material.

According to our earlier investigations of micro-climate (HORVÁTH, 1965), the air and soil temperatures, as well as the relative air humidity are not changed appreciably by a similar covering. The intensity of illumination was reduced by the colourless sheet by about 15 per cent, and by the orange one by 25 per cent. The distribution of spectral energy was not changed by the colourless covering, but the orange covering resulted in reduction of the energy falling in the shorter wave range and increased that falling in the longer one. While the percentage of energy falling in the orange and red wave ranges in the control plots and those covered with the colourless sheet was 39 per cent, that under the orange sheet was 49 per cent (Table 1).

Although not measured, it is probable that the carbon dioxide concentration of the air was increased by the covering, because the air movement was reduced.

Table 1

treatment	violet	blue	green	yellow	orange	red	per cent
control	6	20	27	8	14	25	
colourless plastic sheet	6	19	27	9	13	26	
orange plastic sheet	4	15	24	8	17	32	

The morphological and phenological investigations were carried out on August 8 and 29, and September 7 and 17, 1973, using ten plants from each plot. The leaf surface was calculated by taking into consideration the fresh weight and surface of five leaves from each plot, as well as the fresh weight of all the leaves of the plants collected. Leaves were collected for the histological examinations from the middle region of the stem, on September 7, 1973. The examinations were made from the central part of the middle leaflet of the triple leaf. The material collected was fixed in 60 per cent alcohol and macerated directly or embedded in celloidin for sectoining.

Under the light-microscope, the thickness of the spongy and palisade parenchymas of the leafl, and the length and breadth of the cells of the palisade parenchyma, were measured. From the cell count of the stoma and epidermis, a stomatic index was calculated. In every case, the arithmetical mean of fifty measurements was taken.

The connection between the tissue properties investigated and the production of organic matter was analysed, using a correlation calculation.

A survey and evaluation of results

The main aim of our work was to analyse the connection between the tissue structure of leaves and the organic-matter production. Our results concerning the dry weight of the shoot of a plant, on the basis of a survey on September 7, 1973, are given in Table 2.

Table 2

treatment	dry weight (g)			leaf-surface (sq. cm)
	shoot	crop	total	
control	10.8	3.6	14.4	952.2
colourless plastic sheet	12.5	7.5	20.0	1723.8
orange plastic sheet	14.7	10.0	24.7	2517.2

The data of September 7, 1973 were chosen because it was established during the morphological-phenological elaboration of the material (KÉRI, 1975) that the effects were increasing with time. In the last elaboration, however, the quantity of crop only was given exactly, because many of the leaves had already fallen.

It can be ascertained that the dry weight was increased by covering considerably; this increase was about 75 per cent under the influence of the orange net.

The difference in dry weight first appears in the crop — approximately 200 per cent — and in practical relation the importance of this way of covering is also increased.

Before reporting on the influence exerted on the tissue structure of the leaf, we notice that the leaf surface was considerably increased by covering. As compared with the control, the increase under the colourless net of foil mesh was 90 and under the orange one 170 per cent. The effect can only partly be explained by the lower intensity of illumination. An important factor is — on the basis of our earlier investigations (HORVÁTH, 1965) — also the distribution of spectral energy.

The correlation between leaf surface area and dry weight is positively linear. This is, therefore, not influenced by either light intensity or the distribution of spectral energy (Fig. 1).

Table 3

treatment	thickness of the mesophyll (μ)		percentage			cells of the palisade parenchyma (μ)		
	spongy	palisade	total	spongy	palisade	length (l)	breadth! (b)	l/b
	parenchyma							
1	89.0	103.7	192.7	47	53	24	4.3	
2	103.0	81.4	184.4	56	44	81.7	23.3	3.5
3	90.0	58.3	148.3	63	37	58.4	26.5	2.2

1 = control, 2 = colourless plastic sheet, 3 = orange plastic sheet

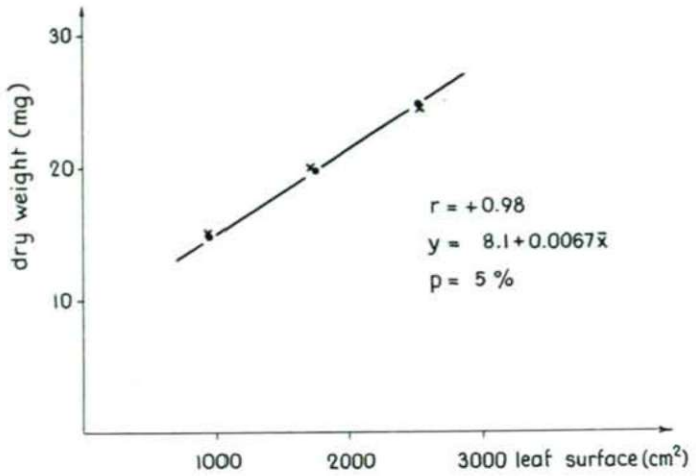


Fig. 1. The results of our histological investigations are summarized in Table 3.

It should be noted that, as a result of covering, the thickness of the leaf-blade is diminished. The diminution caused by the colourless sheet is slight, not more than 4 per cent, but that caused by the orange one is 17 per cent.

This effect — as well as other tissue changes to be discussed below — cannot be explained only by the reduction in light intensity. It is rather to be attributed to a change in the distribution of spectral energy.

The leaves of plants grown in the phytotron in an earlier experiment (HORVÁTH, 1975) in orange light, were thicker than those of plants grown in white, blue or red light. This may be interpreted on an ecological basis, because the light rays belonging to the orange wave range are absorbed to a comparatively lesser extent, ensuring sufficient light energy even in the lower cell-layers of a thick leaf, while the blue and red rays are absorbed to a higher degree, mostly by the upper layers of the leaf mesophyll.

The mesophyll of the leaf of bean consists of the unistratal, well differenctiated palisade parenchyma of heterogeneous structure, and the multi-layer spongy parenchyma.

The cells of palisade parenchyma are columnar, their length-breadth ratio (l/b), is 5 to 1. The spongy and palisade parenchymas comprise approximately identical proportions of the mesophyll.

Under the influence of being covered with plastic sheets, the shape of the cells of palisade parenchyma has considerably changed. They have become less "columnar". This was most evident under the orange sheet where the length/breadth ratio (l/b) was reduced to 2.2. Light is, therefore, one of the main factors involved in the formation of the palisade parenchyma. This has also been shown out by STARZECKI (1962), according to whose statement the main form of the assimilating tissue is the palisade parenchyma. The palisade parenchyma is expressed in leaves receiving intensive light. From among the two kinds of assimilating parenchymas, the spongy parenchyma is, therefore, more general and important.

This is also indicated by our investigations, because the ratio of spongy and palisade parenchymas is considerably shifted — as a result of being covered with the plastic sheets — towards the spongy parenchymas. In the uncovered plots, the proportion of spongy parenchyma was 47 per cent, while under the orange nets it was 63 per cent.

The ratio of spongy parenchyma and the dry-matter production calculated for a single plant are also closely connected (Fig. 2) : $r=0.99$, and the reliability of the connection is : $P=0.01$ per cent.

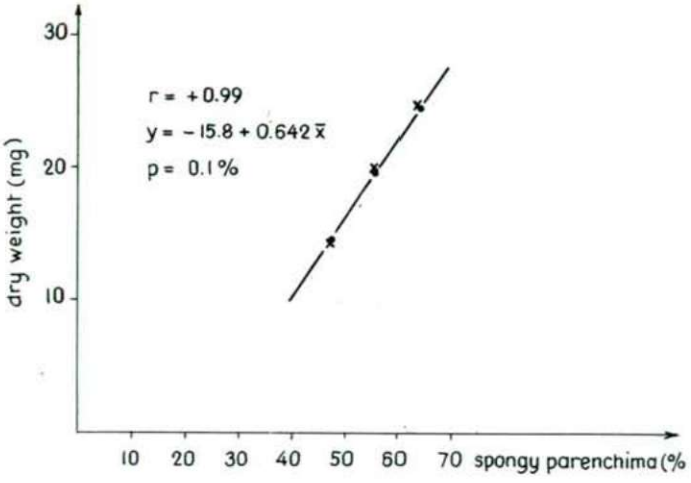


Fig. 2

The change taking place in the structure of the mesophyll is still more considerable if the absolute values of the thicknesses of spongy and palisade parenchymas are taken into consideration. While the thickness of the spongy parenchima has, despite the decrease in the thickness of leaf-blades, changed to only a small extent (Table 3), the thickness of the palisade parenchyma was reduced almost by half.

As a result of the change in form of the cells of the palisade paranchyma, the structure of the mesophyll became more homogeneous, and this may primarily be attributed to the decrease in light intensity. This is also suggested by the comparatively close positive correlation between the change in length-breadth ration and the intensity of illumination (Fig. 3).

The leaves of beans are amphistomatic. The stomata are, apart from a few exceptions, of paracytic type (VAN COTTHEIM 1971), occurring sporadically in the islands of leaf veins. Their number on the upper surface is considerably smaller than on the lower surface. On both upper and lower epidermes, there are to be found unicallular coating hairs and polycellular glandulair hairs. The radial wall of epidermal cells meanders, and the number of cells is considerably lower on the upper surface than on the lower one.

The effect of being covered with the plastic sheets manifests itself first of all on the upper-surface epidermis, and is considerable particularly on the number of stomata. The stoma count is greatly reduced, particularly by the orange covering.

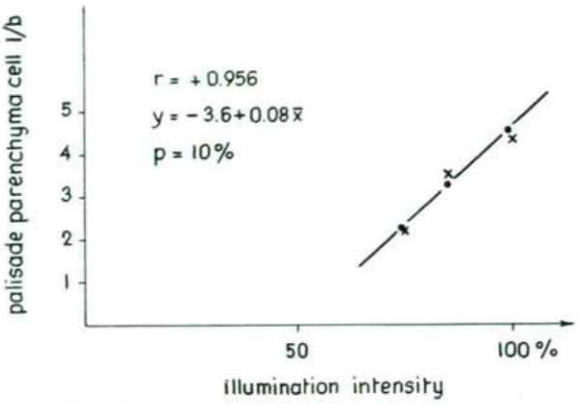


Fig. 3. The changes taking place in the structure of the epidermis are summarized in Table 4.

Table 4

treatment	stoma count sq. mm upper	lower	epidermal cell count sq. mm upper	lower	stomatal index upper	lower
			surface			
control	55.3	375.0	506.9	1066.4	9.8	26.0
colourless plastic sheet	34.5	273.9	433.5	920.2	7.3	22.9
orange plastic sheet	3.9	248.9	329.7	906.9	0.2	21.6

The leaf becomes nearly hypostomatic. The epidermis cell count at the upper surface is also reduced, *i. e.*, the basis cells of the epidermis became larger. The effect on the lower-surface epidemis is smaller. The reduction in the number of epidermal basic cells and in that of stomata can be ascribbed to the decrease in light intensity. A considerable change in the stomatal index, however, is rather to be considered as an effect of the distribution of spectral energy.

* * *

The influence of the covering of colourless or orange plastic sheets, upon the tissue structure of the leaf and the dry weight of the shoot, investigated in field experiments. The intensity of illumination was reduced by 15 and 25 per cent, respectively, as a result of covering. The distribution of spectral energy was also changed by the orange plastic sheets; the percentage of the energy falling to the orange and red wave ranges, rising from 39 to 49 per cent.

It is to be established as a result of our investigations that:

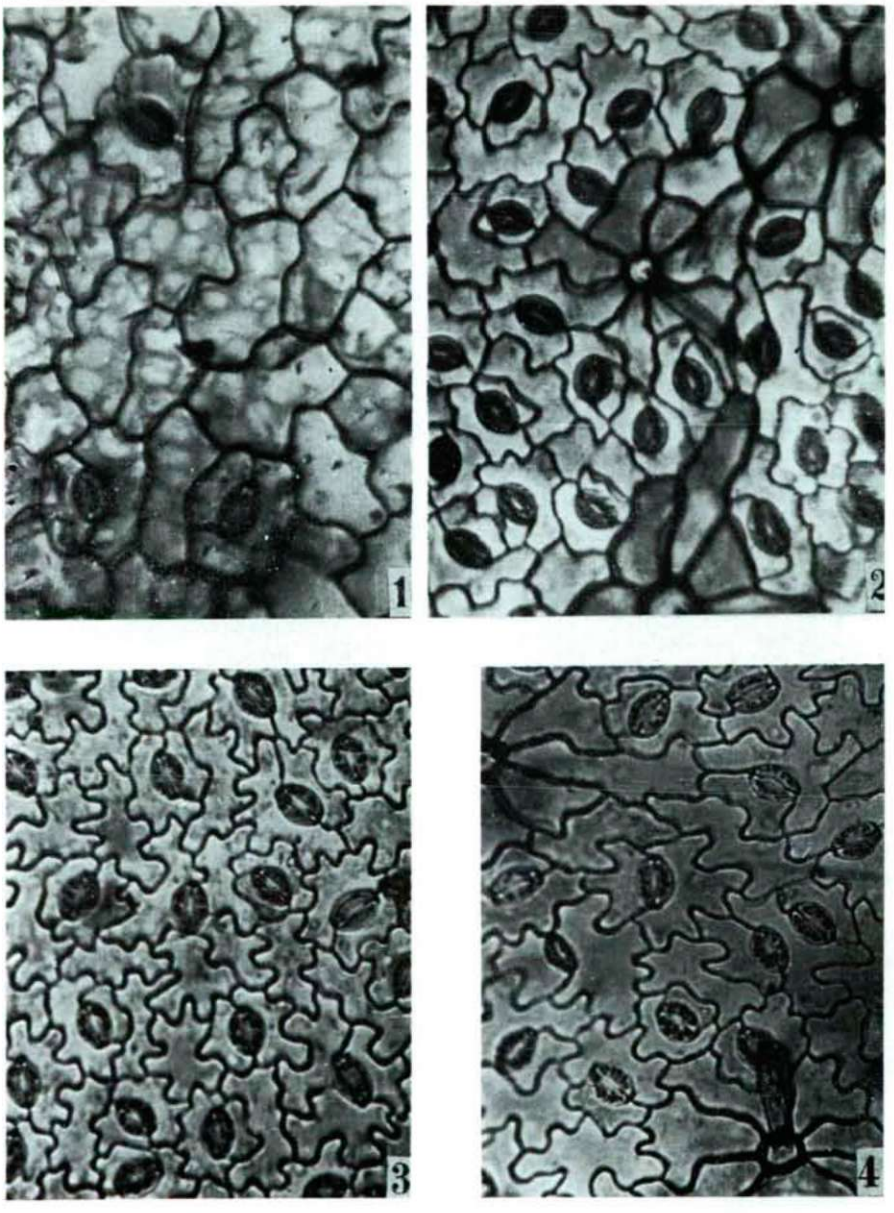
1. The dry weight of shoot and crop, as well as the leaf surface, were considerably increased by covering.
2. The thickness of the leaf-blade was reduced and the proportion of spongy

Plate I. Upper and lower epidermis of *Phaseolus vulgaris L.* ►
(Magnified ×280)
1. Control, upper epidermis
2. Control, lower epidermis
3. Covered with a colourless plastic sheet, lower epidermis
4. Covered with an orange plastic sheet, lower epidermis.

parenchyma increased. The connection between the proportion of spongy parenchyma and the dry weight is close.

3. The shape of the cells of the palisade parenchyma changed, as they became nearly isodiametrical.
4. The number of stomata on the upper surface epidermis, and the epidermal cell count, were reduced. As a result of the orange covering, the amphistomatic leaves became almost hypostomatic.

Plate 1



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RAPID DETERMINATION OF DROUGHT-RESISTANCE OF NEW RYE, MAIZE AND LUPINE VARIETIES WITH THE LIVE-WILTING PROLINE TEST

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Abstract

In six varieties of proline-type rye, in two of non-proline-type maize, and in five of lupine, apart from measurement of the proline content of the water-deficient, isolated shoots, the concentrations of the free total amino-acid and of the soluble total protein were also determined. The proline concentration of the water-deficient isolated shoots turned out to be a positive correlation with the amount of the total amino-acid and the soluble total protein, and with the degree of drought-resistance. The new complex method, after some further experiments, may therefore be suitable for evaluating the drought-resistance of new varieties of plants.

It also turned out that, as a result of a water-deficiency of the same degree in the isolated shoots, no qualitative difference could be demonstrated in the free amino-acid compositions of plants belonging to the same species. However, whereas the amount of proline predominates among the free amino-acids of the proline-accumulating species (*e.g.* rye), among the non-proline-type species (*e.g.* maize and lupine) the asparagine concentration may achieve the highest level.

Introduction

It was established in our previous work that, as a result of a strong water-deficiency, the essential amino-acids, asparagine and particularly proline accumulate very considerably in the green shoots. At the same time, the total amount of the free protein-producing amino-acids also increases to two to three times as much as in the (non-water-deficient) control (PÁLFI, 1968a b). In the course of investigations into capsicum, tobbaco, wheat, barley, and rye plants, it turned out that the drought-resistance of the individual varieties is proportional to the amount of free proline accumulated in the leaves (PÁLFI, 1969; PÁLFI and JUHÁSZ, 1971; KUDREV, 1970; LEWITT, 1972; SINGH and ASPINALL, 1972). On the basis of quantitative measurements of the proline content in the leaves of plants suffering from a water-deficiency, a simple procedure was elaborated in order to decide the drought-resistance of the individual varieties the new method being named the "proline test" (PÁLFI, 1969; PÁLFI and JUHÁSZ, 1971; PÁLFI et al., 1973).

It was also established that, as a result of a water-deficiency and live-wilting conditions of the same degree, quite different proline amounts accumulate in the different plant species.

Starting from all these data, the cultivated soft-stalk plants were divided into two groups: 1 = proline-type species; 2 = non-proline-type species (PÁLFI et. al.,

1974a b; 1975a b). A species is named of proline-type if it is live-wilted isolatedly, *i. e.* the free proline content of the shoots or leaves suffering from a strong water-deficiency reaches or exceeds 10 mg in 1 g dry matter (1.0 per cent of the dry matter).

Below this quantity the species is no longer of proline-type. From among fifty cultivated soft-stalk plants only seventeen nonproline-type species were found. The majority of the cultivated plant species are therefore of proline type (PÁLFI et al., 1974a b).

In the present experiment we have striven to clarify how, apart from proline, the total amount of the free protein-forming amino-acids and the concentration of the soluble total protein develop in the course of live-wilting of the isolated shoots and leaves, inducing a strong water-deficiency.

Can this qualitative difference be demonstrated as a result of the strong water-deficiency in the free amino-acid composition of the isolated shoots of varieties belonging to the same species?

To study the problem, we investigated altogether twelve varieties of two plant species of non-proline-accumulating type (lupine and maize) and of one species of proline-type (rye).

In the course of the experiments, two varieties of hybrid maize were applied as guides; the drought-resistances of these are well-known, because the results of culture experiments during several years have shown a considerable, one-direction deviation in this respect (PINTÉR et al., 1976).

Materials and Methods

The new rye (*Secale cereale L.*) and Yellow lupine (*Lupinus luteus L.*) varieties were improved by M. BRUMMUND and W. BÖLKE in a loose sandy soil, in "VEG Saatzucht Bornhof, Saatzuchtstation Bocksee" (Kreis Waren, DDR). The production and preservation of the hybrid maize varieties (*Zea mays L.*) was performed by JÁNOS NÉMETH in Szeged, in an adobe field soil, in the establishment of the Cereal Research Institute.

The names (symbols) and stages of development of the varieties investigated are as follows:

Rye: From three sorts of rye, shoot samples were taken immediately before flowering. The variety symbols are: R_1, R_{33}, R_{81}.

The shoots of the other three rye varieties were collected in the phase of flowering. The symbols are: R_{131}, R_{132}, R_{139}.

Lupine (Lupinus): On budding, two varieties of lupine shoot samples were taken, their names being: 1 = Bornhof; 2 = Refusanova. The names of the other three varieties of lupine taken on flowering are: 1 = Afus; 2 = Borluta; 3 = Pilaf = (Bocksee).

Maize: Two varieties were investigated, but in three phases of development. The two hybrid maize varieties are:

1. BcSK-5/a; its symbol: W64A×Oh43. In Jugoslavia it is a variety recognized by the State and in Hungary it is allowed for raising. It demands water and is only slightly drought-resistant.

2. KSC.360; its symbol: A90×153R. It is a Hungarian-improved variety, recognized by the State. It needs only little water. According to the experimental results of PINTÉR et al., (1976), it is much more drought-resistant than the previously-mentioned Jugoslav variety. For the two maize varieties full shoots were isolated twice for live-wilting (at the ages of seven and eleven leaves), while on the third occassion only leaves were detached and processed (from among the 14-leaf shoots the eleventh leaves counted from below).

The average result was the live-wilting of 20 isolated shoots each of the rye and lupine varieties and 10 of maize. The shoot groups were put on trays according to varieties and the live-wilting was performed at a temperature between 20 and 28 °C. The relative air humidity was 60 to 70 per cent, and the constant illumination 2000 lux. The isolation of rye and lupine shoots lasted for two days and that of maize for four days. (The live-wilting of isolation

leaves was carried out only for three days). During this time, the water content of the shoots had to be reduced by 60 to 70 per cent.

The analyses were performed from the pulverized matter of the plants fixed (and dried) immediately on being detached, and after being live-wilted at 70 °C.

For analysis of amino-acids, 200 mg dry matter was homogenized with 1 g quartz sand, in a mortar, with 20 ml 30 per cent ethanol, and leached twice out of the mortars dishes into centrifuge tubes from the residue of the 20 ml. The homogenizate was purified by being centrifuged. Finally, as a result of evaporation and wetting losses, we obtained 18 ml extract. This was the starting basic solution quantity for all analysis and concentration calculations.

The method of measuring the free total amino acid with a universal standard was published earlier (PÁLFI et al., 1972).

In proline determinations a phenol-water (4:1) mixture was used as solvent. After isatin development (Figs. 3 and 4) and the eluation of spots, the extinctions were measured with a spectrophotometer.

The soluble total protein originating from the leaves of the live-wilted shoots was measured by nephelometry, according to COLOWICK and KAPLAN (1957); with some modifications. From 0,2—0,5 g living material, the proteins of the extracts (0,5 or 1,0 ml) made with 20 ml Tris buffer of pH 7,5 were reacted with 4 ml portions of three kinds of precipitating solutions:

1) 5% trichloracetic acid; *2)* 2,5% sulphosalicilic acid; *3)* 0,7% $K_4Fe(CN)_6$ + 0,3 ml concentrated acetic acid.

By variation of the quantity of the starting protein-extracts, the turbidity is adjusted so that the 4 ml reagent should induce only the mild, homogeneous opalescence of the solution. Agglutination, precipitation and fast deposition may not occur. The extract amount tested with trichloracetic acid is generally optimum for the other two protein precipitants, as well.

For the calibration curve, a standard series of "Bovine blood serum albumin" (5, 10, 15, 20 and 30 mg) was measured out and dissolved in 20 ml Tris, and the extinctions of the solutions were measured.

The results of three repetitions were averaged per reagent, and the final result was obtained after the partial results achieved in this way were averaged again.

If the mean error in the average results for repetitions of identical samples was larger than ±5 per cent, then the whole analysis was repeated.

Results and discussion

First we wanted to clarify whether there is any qualitative difference in the composition of free amino-acids as a result of the strong water-deficiency provoked by live-wilting the isolated shoots of the improved varieties belonging to the same species. Of the prepared chromatograms, an 18-strip paper developed with ninhydrin is demonstrated, involving the extracts of three varieties of lupine, three of rye, and two of maize (Fig. 1). In the evaluation of the chromatogram, it is also to be taken into consideration that only the growth and live-wilting of the varieties belonging to the same species took place at the same time, together and under identical conditions (a real result is therefore only obtained in the case of comparing the varieties belonging to the same species).

It is to be seen in Fig. 1 that no qualitative difference was induced in the composition of the free amino-acids of the varieties belonging to the same species, as a result of a water-deficiency of the same degree. An essential quantitative difference was found only in the proline and asparagine concentrations of the individual species. Most proline is contained in the rye varieties (a species of proline type), and asparagine is mostly accumulated in the lupine and maize varieties. According to CREACH et al., (1974) the large amount of asparagine in the maize plant acts as an internal carbon dioxide reserve, although maize is overwhelmingly "malat-forming". In respect of the chromatogram in Fig. 1 is to be noted that if the extent and colour

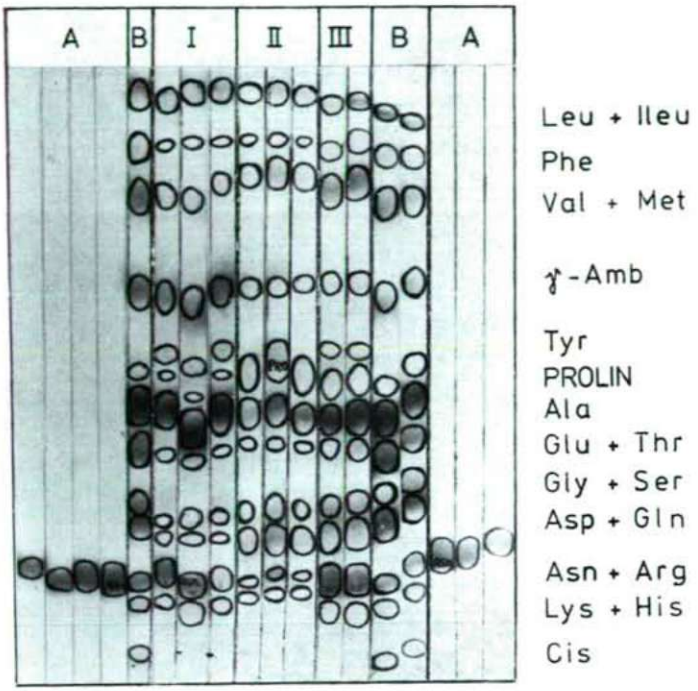

Fig. 1. Qualitative composition of free amino acids of the Yellow lupine, rye, and maize varieties as a result of live-wilting connected with a strong water-loss. The live-wilting of the lupine and rye varieties took place with isolated shoots, but with isolated leaves for the maize varieties. Ascending chromatogram. Solvent: butanol-acetic acid-water (3:1:1). Ninhydrin development, fixing with copper salt.
A = Asn standards: 5, 10, 15, 20, 30, 20, and 10 µg;
B = Universal standards with 30, 45 and 30 µg total amino acid content;
I = Yellow lupine varieties: Afus, Borluta, and Bocksee;
II = Rye varieties: R_1, R_{33}, and R_{st};
III = Hybrid maize: W64A × Oh43 (foreign) = BcSK 5/a;
A90 × 153R (Hungarian variety) = KSC 360.

intensity of the asparagine spots of the extracts are compared with those of the standards, then an approximative evaluation is possible concerning the absolute quantity.

The question may arise, however, as to whether the varieties run on a single strip can give evaluative results. As regards this question, it must be taken into consideration that the varieties of all species were run on a separate chromatogram, too, on 3 to 4 adjacent strips, *i.e.* in 3 to 4 repetitions. In Fig. 2 a chromatogram is demonstrated in which the extracts two varieties of Yellow lupine were developed in a uniform quantity, in four adjacent repetitions. At the edges of the paper, the universal standard appears in three different quantities.

It turns out from Fig. 2 that, if identical quantities of an extract made from the same variety are run in four repetitions, we may obtain uniform separations and spot sizes. The method is therefore reliable. The further important conclusion at

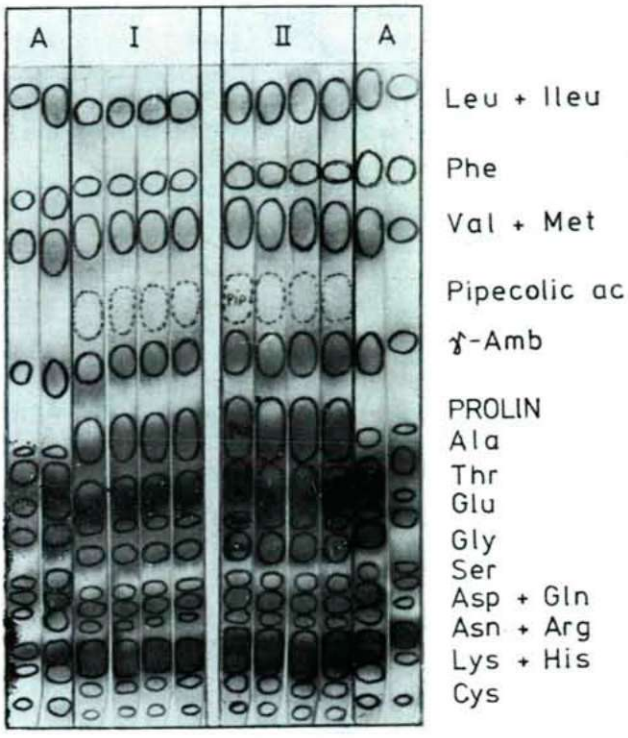

Fig. 2. Qualitative composition of free amino acids of the two lupine varieties, as a result of the live-wilting of the isolated shoots, connected with a strong water-loss. The chromatogram was made with the same butanol solvent and ninhydrin development as recorded in the previous Figure. The extracts of both varieties were run on four adjacent strips, *i. e.* in four repetitions.
A = Universal standards, in sequence, from the left: 15, 30, 45 and 30 µg total amino-acid content;
I = Bornhof variety (4 repetitions);
II = Refusanova variety (4 repetitions).

present is that no qualitative difference is to be observed between the amino-acid compositions of the two varieties.

It is also to be seen in the chromatogram that the spots of the "Refusanova" variety (the four repetitions on the right) are generally somewhat larger than those of the "Bornhof" variety, on the left. The total amino-acid concentration of the "Refusanova" variety is therefore larger. In Fig. 2, a cyclic amino-acid is also present: pipecolic acid, which is not a protein-former, but is characteristic of legumes.

As regards Fig. 1 and 2, it may be stated that, if the proline is developed with ninhydrin, they only give spots of pale (light yellow) colour. Further, this spot cannot be eluted, either to be measured colorimetrically. In the quantitative measurement of proline, we have therefore applied the highly sensitive isatin, which forms an intense, dark-blue spot with proline. In Fig. 3 a chromatogram is visible which was developed with isatin for measurement of proline quantities. It illustrates the extracts

of three varieties of rye, in three repetitions each. In addition, proline standards as well were run on the same paper.

In Fig. 3 it is discernible that, from among the free amino-acids of rye varieties, proline gives dark (blue) spots of very considerable size (rye being a species of proline-accumulating type) and, if a phenolic solvent is applied, it is fully separated from the other amino-acids. From the chromatogram it is visible even to the naked eye that the proline and total amino-acid concentrations of the rye variety run in the middle (R_{33}) are higher than those of the other two varieties. It is also seen from the chromatogram that — apart from proline — the other amino-acids form only pale spots of very little extent, as they respond poorly to the isatin developer.

In the following, we shall examine what spot intensity is given by proline, and what is the quantity and relation of the other amino-acids, as compared with proline, in the case of the phenolic running on paper of the extracts of lupine varieties belonging to the non-proline type, and of their isatinic development (Fig. 4). It must be mentioned in advance, however, that in the case of varieties belonging to the non-proline type — *e.g.* lupine — it is necessary to apply (3 to 4 times as much extract as from the varieties of proline type) for the proline to appear in a measurable quantity.

It turns out from Fig. 4 that in the case of the extracts of the isolatedly live-wilted, that is to say strongly water-deficient shoots of lupine-varieties, the largest

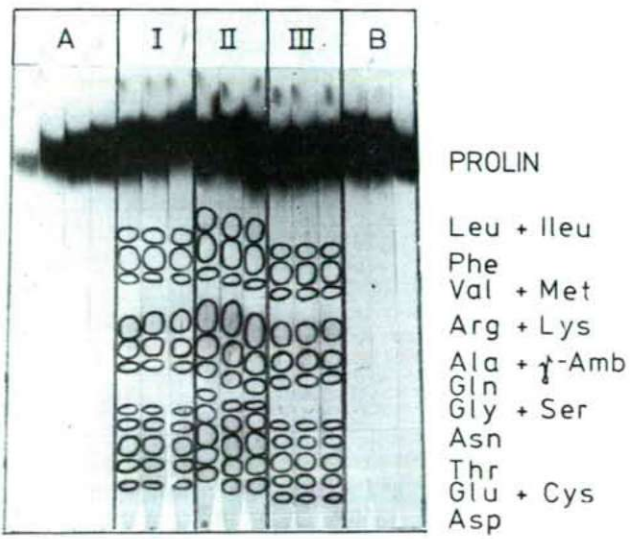

Fig. 3. Separation of the free amino-acids of the rye varieties belonging to the proline-accumulating type, and the quantitative determination of proline in the case of applying a phenol-water (4:1) solvent. Developer: isatin solution, which reacts strongly with proline. Identical quantities of all varieties were run on three adjacent strips, i. e. in three repetitions. The strong water-deficiency of the varieties was induced by live-wilting the isolated shoots for two days.
A and B = proline standards, starting in sequence from the left: 5, 10, 15, 20; and 40, 30, 20 μg;
I = rye variety R_1; II = rye variety R_{33}; III = rye variety R_{st}.

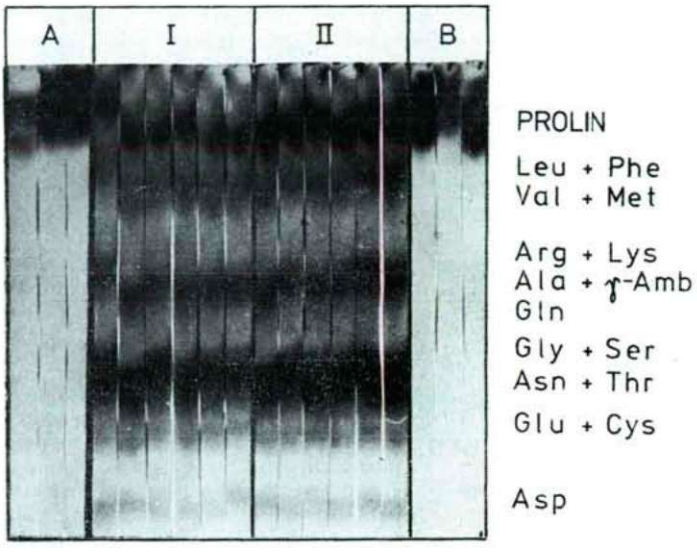

Fig. 4. Determination of the proline in the two varieties of Yellow lupine of non-proline-type, with a paper-chromatographic, eluation method. Live-wilting took place with isolated shoots. Identical quantities of the extracts of the lupine varieties were run on six adjacent strips each, i.e. repeated six times. The solvent was phenol-water, and the developer was isatin, as in the previous Figure. On both sides of the chromatogram, on the three extreme strips, proline standards were run.
A and B = proline standards in sequence from the left: 5, 10, 15; and 20, 5, 10 μg;
I = Bornhof variety; II = Refusanova variety.

and most intensive spot is not given by proline; it is a common spot of asparagine + + threonine. It was established by ATKINS et al., (1975) that in the case of lupine and most legumes the most N-containing important product of nitrogen-fixation and nitrate reduction is asparagine. In addition, asparagine similarly acts as a primary N-source of protein synthesis. Proline does not always predominate, therefore, among the free amino-acids of the plant species not belonging to the proline type. At any rate, in this method, if the optimum quantity of extract was applied, the amino-acids are still reasonably separeted and proline is present in a quantity that can be eluted well for colorimetric measurement.

It is also to be seen in Fig. 4 that proline is contained in a major amount by the extract of the "Refusanova" variety (strip 6, on the right on the paper).

Before reporting the results of our quantitative measurements, it is to be mentioned that for any variety of every species, on isolating a group of shoots (control), we immediately measured the fresh matter. After being fixed, this was then dried and, after live-wilting for two, three or four days, the wilting weights were measured too. It was established from these weights whether live-wilting could be finished, as the wather-deficiency had already achieved 65 to 70 per cent compared with the fresh weights. After starting from an identical weight of fresh matter, as well as of live-wilted matters of the same water-loss, the dry-matter contents were also measured for all varieties. It was established that, as regards the dry-matter contents measured in this way, we obtained no characteristic difference

according to variety, whether we had started from fresh or from live-wilted matter. The free amino-acid contents related to 1 g dry matter give, therefore, a correct basis for comparison. Taking into consideration that samples were taken from the two hybrid maize varieties three times, primarily the data of these are reported here (Table 1).

The provocation of the water-loss of the isolated full shoots was carried out in the case of maize, with live-wilting from the third till the sixth day. However, even during the six days, the reduction of the water-content in the isolated shoots did not reach 65 to 70 per cent, but amounted only to 55 per cent. At the same time, the largest free amino-acid and total-protein contents were achieved in the shoots live-wilted for four days. These data are therefore given in Table 1.

Table 1. The free proline, total amino acid and soluble total protein contents of the isolated shoots and leaves of two hybrid maize varieties, as a result of a strong water-loss (live-wilting). At the 7- and 11-leaf ages, the full shoots were isolated; their live-wilting, inducing a strong water-deficiency, lasted with constant illumination for four days. At the 14-leaf age, the eleventh leaves were isolated, counted from below, and their live-wilting lasted for three days. A real basis for comparison is only given by the results of the varieties equally developed, raised under identical conditions, and live-wilted together, (varieties separated from each other by horizontal lines in the Table)

Hybrid maize	Development of shoots at the time of isolation	Proline content from the live-wilted sample; mg/g dry mater	Total amino-acid content, mg/g dry matter		Soluble total protein; live-wilted matter mg/g
			From shoots		
			fixed on detaching	live-wilted	
Hungarian hybrid KSC 360 A90×153R	7-leaf shoots	1,1	9,9	60,3	39,6
Foreign hybrid BcSK 5/a W64A×Oh43	7-leaf shoots	1,2	9,0	52,7	33,1
Hungarian hybrid KSC 360 A90×153R	11-leaf shoots	1,2	20,4	71,1	45,8
Foreign hybrid BcSk 5/a W64A×Oh43	11-leaf shoots	1,1	20,4	60,6	37,5
Hungarian hybrid KSC 360 A90×153R	isolated leaves	3,9	16,8	49,8	42,9
Foreign hybrid BcSK 5/a W64A×Oh43	isolated leaves	3,2	14,4	41,0	35,2

It is clear from Table 1 that, in the course of the live-wilted water-loss of the isolated full shoots, in the case of maize, at the times of both the 7- and 11-leaf developments only a very small proline amount was accumulated. In addition, there was no characteristic difference between the proline contents of the two varieties investigated, either. Therefore, in the course of sampling 3, we have no longer isolated full shoots, but only leaves (counting leaf 11 from below in the shoots with 14 leaves). In the course of live-wilting the isolated leaves, we have already achieved a 70 per cent water-loss in three days, as compared with the water-content of the freshly-isolated leaves.

It can be established from Table 1 that, as a result of this strong water-loss of the isolated leaves, the proline concentration became three times higher as compared with the isolated shoots (1.2 : 3.9). At the same time, there is a considerable difference between the proline contents of the varieties as well. The Hungarian improved variety, *i.e.* "KSC 360" accumulated 21.8 per cent more proline than the variety of foreign origin, "BcSK 5/a".

This result at all events supports our previous finding (PÁLFI et al.,1973, 1974a, b) that maize is not a proline-accumulating type because, even as a result of a strong water-deficiency the proline concentration of the leaves does not amount, to 10 mg/g dry matter.

It is to be seen from Table 1 that in the free total amino-acid contents of shoot- and leaf-samples fixed and dried immediately after being detached, there is hardly any characteristic difference between the two varieties. However the total amino-acid amounts of the samples taken at the times of different developments differ from each other uniformly and strongly in both varieties. The total amino-acid content of the first isolated 7-leaf shoot sample for instance, is more than two times lower than that of the shoot sample taken on the second occasion. Further, as compared to this, the total amino-acid content of the isolated leaves is even smaller (by 25 to 30 per cent). However, we are mainly interested in the total amino-acid content, formed primarily as a result of the live-wilting water-loss of the isolated shoots.

Table 1 shows that the amount of the free total amino-acids accumulated as a result of the strong water-deficiency, at all three developmental and sampling-stages was larger for the Hungarian variety "KSC 360" than for the foreing variety "BcSK 5/a" (the difference falls between 14.4 and 21.4 per cent).

In Table 1, it is demonstrated that in the course of analysing the live-wilted matter of a strong water-loss, in respect of the soluble total protein, too, for all three samplings the larger amounts were given by the Hungarian improved variety as compared with the foreign one (the difference falls between 19.6 and 22.1).

It can therefore be established from the data of Table 1 that the free total amino-acid and soluble total-protein contents of the variety showing a stronger proline concentration as a result of the strong water-deficiency, i.e. the Hungarian "KSC360", also achieved considerably higher levels than those of the foreign variety, "BcSK 5/a". As the drought-resistances of both maize varieties investigated are already known from the results of raising experiments (PINTÉR et al., 1976), it can be stated that the amounts of the free total proline, total amino-acid, and soluble total protein at higher level, accumulated as a result of the strong water-loss, are connected with the higher degree of drought-resistance.

In estimating the drought-resistances of maize varieties, we can also consider

that, in the course of isolating, live-wilting, and analysing the young but already fully-developed leaves, taken from the upper one-third of shoots in the state of development before tasselling, a major proline content can be achieved and that the difference between the varieties may be more considerable.

It was established by JOVANOVIC (1975) that the crop of hybrid maize was most influenced by the amount of precipitation in the period lasting from the 9-leaf stage till tasseling. This result supports our suggestion that, in order to determine drought-resistance, the sample taken in the phase before the development of tasselling is most suitable because the maize plant is most sensitive to a water-deficiency at this time.

GUPTA and KOVÁCS (1974) put in an air-conditioning plant for four days maize plants raised under glass in a culture-vessel until their 5-leaf stage and induced in these a strong water-deficiency. They then set out the seedlings in the field and, during the raising of the plants, determined their drought-resistance. The results agree with our finding that the considerable differences during the determination are given by the maize plants exposed to a strong water-deficiency for four days.

In the following, we pass to an analysis of the rye and lupine varieties. In an evaluation of the results of Table 2, however, it is to be taken into consideration that real data for comparison are given only by the analysed data of the live-wilted shoots isolated at the same time from among the shoots raised under identical cultural conditions, belonging to the same species and showing the same development. The data corresponding to these conditions are separated from one another by horizontal lines drawn between species and varieties. Correspondingly, the rye and lupine varieties at the two stages of development form separate groups in respect of evaluation (Table 2).

In Table 2, the first three, *i. e.* the free proline, total amino-acid and soluble total protein contents of rye variety R_{33}, for the isolated shoots, live-wilted for earing, resulted in much higher values than the other two, varieties, R_1 and R_{st} (R_{st} = standard variety). At the same time, the higher-level proline and total amino-acid contents of variety R_{33} are also reflected by the chromatogram of Fig. 3. Similarly, one of the three rye varieties, R_{132}, showed a considerably higher level, in respect of both proline and total amino-acid and soluble total protein. The other two rye varieties R_{131} and R_{139}, afforded fairly uniform concentrations as compared with each other concerning the materials investigated.

Similarly to the analyses of maize varieties, therefore, it can also be stated for the rye samples that the same variety gave characteristically higher values in regard to the total amino-acid and the soluble total protein, as well, in which the proline concentration of the isolated shoots rose to a higher level during the strong water-loss. It can be established from the proline amounts of the rye varieties that the rye species belongs to the proline-accumulating type: as a result of a strong water-deficiency, for all the six varieties investigated, the proline concentration of their isolated shoots exceeded the critical 10 mg/g level.

SINGH and ASPINALL (1972) investigated the drought-resistances of ten barley varieties, belonging similarly to the proline type. The rapid formation of a strong water-deficiency was induced by wetting for three days the root medium of the plants raised in a culture-vessel for a period of three weeks with a hypertonic solution of polyethylene glycol (-20 bar). SINGH and ASPINALL demonstrated, as a result of the strong water-deficiency of barley at the same level, very different proline concentrations in the leaves (from 9.0 up to 24.1 mg/g dry matter) according to varieties.

Table 2. The free proline, total amino-acid and soluble total protein contents of the isolated shoots of the rye and Yellow lupine varieties, as a result of a strong water-loss (live-wilting). Live-wilting lasted for two days with constant illumination. (Only the developments of the species and varieties separated from each other by horizontal lines are identical.)

Species and varieties	Development of shoots at the time of isolation	Proline content from the live-wilted sample; mg/g dry matter	Total amino-acid content, mg/g dry matter		Soluble total protein; from live-wilted matter mg/g
			From shoots		
			Fixed on detaching	live-wilted	
Rye: R_1	on earing	15,2	11,2	23,6	27,6
Rye: R_{33}	on earing	22,8	13,5	32,5	33,5
Rye: R_{81}	on earing	12,5	11,6	24,3	27,9
Rye: R_{131}	on flowering	12,7	12,7	24,6	25,7
Rye: R_{132}	on flowering	20,3	15,0	30,9	31,4
Rye: R_{139}	on flowering	11,5	12,8	23,8	25,8
Lupine Bornhof	on budding	3,4	16,3	47,2	36,7
Lupine Refusanova	on budding	4,8	16,8	52,8	44,2
Lupine Afus	on flowering	3,5	15,4	39,7	35,5
Lupine Borluta	on flowering	4,2	15,9	45,6	41,8
Lupine Bocksee	on flowering	3,0	15,1	34,2	32,1

The authors proved with their field-growing experiments with the same ten barley varieties that drought-resistance of the varieties increases in direct proportion to the rise in the proline concentration. This fact has already been ascertained by us in our former investigations and by other authors, as well (PÁLFI, 1969; PÁLFI and JUHÁSZ, 1971; PÁLFI etal., 1973; ASPINALL et al., 1973; WALDREN and TEARE, 1974).

Returning to the data of Table 2, it is clear that from among the two kinds of lupine samples taken on gemmation, the proline, total amino-acid, and soluble total protein concentrations of the Refusanova variety show higher values than those of the Bornhof variety. These results can also be concluded from the spot sizes of the chromatograms in Fig. 4.

In Table 2., the results of the three kinds of lupine varieties taken on flowering show a gradual differenciation: the proline, total amino-acid and soluble total protein concentrations of the Bocksee variety are the smallest. Those of the Afus variety are already higher, but those of the Borluta variety achieved the highest level. The results on isolated lupine shoots, taken on budding and flowering and exposed

to a strong water-deficiency, similarly to the data obtained for the rye varieties, indicate that if the proline concentration of a variety is higher then the total amino-acid and soluble total protein amounts of the same variety rise to a higher level, as well.

ASPINALL et al., (1973), BATES et al., (1973), LEWITT (1972), SINGH and ASPINALL (1972) and WALDREN and TEARE (1974) determined the degree of drought-resistances of plants on the basis of the concentration of accumulated free proline. They did not take into consideration whether the plants investigated were of proline-accumulating type or not. This new classification has not been applied by other authors apart from ourselves as yet.

It is to be seen from the results (Tables 1 and 2) that the isolated shoots of the species classified into the non-proline type accumulated only a relatively small quantity of proline as a result of a strong water-deficiency. In cases like this, the possibility of errors in analyses increases. It seemed to be advisable to determine, not only the proline, but also the free total amino-acid and soluble total protein contents which amounted, as a result of the water-deficiency, to 200 to 300 per cent of the control well supplied with water. According to our results, not only the amount of free proline accumulated owing to the water-deficiency is in correlation with the drought-resistance of the variety investigated, but also the free total amino-acid and soluble total protein concentrations if live-wilting was carried out for the required time and under the optimum conditions. Therefore, after being further investigated, this complex method seems to be suitable for the rapid evaluation of the droght-resistances of the new plant varieties created by the improvers.

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EFFECT OF BUTACHLOR (2-CHLORO-2', 6'-DIETHYL-N-) BUTOXYMETHYL(-ACETANILIDE) ON THE BASIPETAL TRANSPORT OF EXOGENOUS INDOLE-3-ACETIC ACID IN MAIZE SEEDLINGS

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Abstract

In maize seedlings grown in a culture solution, the basipetal transport of indole-3-acetic acid labelled on the carboxyl group, which had been located on the leaf surface, was delayed by butachlor (2-chloro-2', 6'-diethyl-N-)butoxymethyl(-acetanilide) in a concentration of 20 ppm. Inhibition of the transport led to the accumulation of indole-3-acetic acid in the region of the accessory roots.

Introduction

Butachlor, a chloracetanilide, is a selective herbicide which is employed primarily pre-emergently against mono- and dicotyledonous weeds in rice, cotton and soya cultures, but which can also be used for the treatment of maize, sunflower and sugar-beet.

The α-chloracetanilides are germination-inhibiting herbidides, but their herbicidal effect is not unambiguously a consequence of the germination-inhibition. In many plants the herbicide inhibits not the germination, but the normal growth following the germination. The growth-inhibiting effect extends to the cell-division and elongation (HICKEY, et al. 1974; DHILLON and ANDERSON, 1972; ESHEL, 1969; EDMONDSON, 1969; KEELY, 1972).

The growth-inhibiting effect is in all probability closely connected with the inhibitory effect of the α-chloracetanilides on protein synthesis (JAWORSKI, 1969; MORELAND, 1969; DUKE, 1967, 1975).

Our observations on maize plants indicate that butachlor induces morphological changes primarily in the roots, in so far as it decreases the number of second-order branchings and increases the number of adventitious roots formed at the first internodes. Since the increase in the number of adventitious roots is indicative that the change takes place in the auxin household of the plants on herbicide treatment, we carried out experiments to study the changes in the transport and metabolism of indole-3-acetic acid (IAA) in the organs of the treated maize plants. In the present paper we deal with the effect of butachlor on auxin transport.

Materials and Methods

As experimental plants, 12-day-old seedlings of *Zea mays* L. cvar. *Keszthelyi* SC. were used, which had been grown in a four-fold diluted Knop culture solution (pH 6.8) after pregermination for 3 days in a thermostat at 25 °C. Five seedlings were placed in each of the vessels, which contained 450 ml culture solution. The experiments were carried out under controlled conditions in a "CONVIRON" growth chamber, with 14 hours of daylight, a daytime temperature of 24 °C, a nighttime temperature of 18 °C, and a relative humidity of 60%.

The radioactive butachlor was synthetized in the Isotope Laboratory of the Biological Research Center of the Hungarian Academy of Sciences. The specific activity of the preparation was 0.61 Ci/mmole.

The correlation between the herbicide effect and the IAA transport was investigated under the following experimental conditions.

1. Uptake of ^{14}C-butachlor. At the age of 12 days, the seedlings were placed in a four-fold diluted Knop solution containing 20 ppm unlabelled butachlor. A total amount of 50 μci of butachlor was added to the culture solution in each culture vessel. In the course of the sampling, the plants were placed in an electric drying press and the autoradiograms were prepared on "Forte Medifort R" medical X-ray film with an exposure time of one week. The same procedure was employed for every sample.
2. Uptake of ^{14}C-IAA. In the form of 0.1 ml of a 50% ethanolic solution, and in a total amount of 0.5 μCi per plant, ^{14}C-IAA labelled on the carboxyl group was transferred to the third, youngest leaf of the 12-day-old, three-leaved seedlings growing in the Knop culture solution.
3. Transport of ^{14}C-IAA with the simultaneous use of hormone and butachlor. A four-fold diluted Knop solution containing 20 ppm butachlor was prepared, and the 12-day-old seedlings were treated with ^{14}C-IAA as described in point 2, in parallel with their transfer to the herbicide-containing culture solution.
4. Transport of ^{14}C-IAA in plants pretreated with butachlor. The procedure was similar to that described in point 3, but the labelled IAA was transferred to the leaf 24 hours after the herbicide treatment.

Results and discussion

The transport and translocation of the exogenous IAA were studied with maize plants treated with butachlor via the roots. The use of labelled butachlor was of benefit for the correct selection of the intake time of the IAA into the plants and for the investigation of the translocation of the butachlor. In the experiments the transports of the two compounds were studied when employed separately and in combination.

1. Uptake of ^{14}C-butachlor

The uptake of the labelled herbicide via the root can still barely be perceived in the sample taken 2 hours after the treatment; merely the grain displays a slight labelling, which is probably connected with the higher oil content. Even 12 hours later only the roots contain labelling (Fig. 1). The translocation of the butachlor is relatively slow; in practice, the butachlor does not enter the aboveground parts.

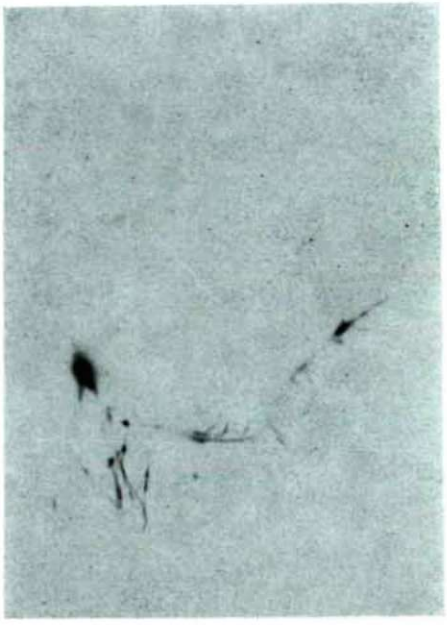

Fig. 1. Transport of ^{14}C-butachlor in 12-day-old maize seedlings. Distribution of radioactivity in the seedling 2 hours after treatment.
The bulk of the radioctivity is accumulated in the grain, with a small amount in the root. The butachlor is not translocated into the aboveground parts later either. Activity of butachlor added to culture solution: 1.1 μci/ml. The autoradiagram was prepared on, "Forte Medifort R" film. Exposure time: 1 week.

2. Uptake of ^{14}C-IAA

Two hours after the treatment, the labelled IAA taken up via the leaf is translocated throughout the entire length of the maize seedling. And enhanced radioactivity compared to the untreated specimens can not be found in the zone of the adventitious roots (Fig. 2).

3. Combined uptake and translocation of IAA and butachlor when applied at the same and at different times

In the experiments, unlabelled butachlor was added to the culture solution, and 1-^{14}C-IAA was transferred to the leaf. If the two compounds were applied simultaneously, the auxin transport is unimpeded in the 2-hour sample (when the herbicide uptake is still not appreciable). 6 and 12 hours after the treatment, when the butachlor has already accumulated in the roots, the radioactivity is accumulated in the adventitious root zone and above it (Fig. 3).

If butachlor pretreatment is employed before the addition of labelled IAA, in the 2-hour sample the translocation of auxin is inhibited compared to that of the plant maintained in herbicide-free culture solution, and the roots barely display radioactivity. In the 6 and 12-hour samples a significant labelling accumulation can be observed in the nodes above the adventitious region. This originates from inhibition of the basipetal transport of the IAA (Fig. 4).

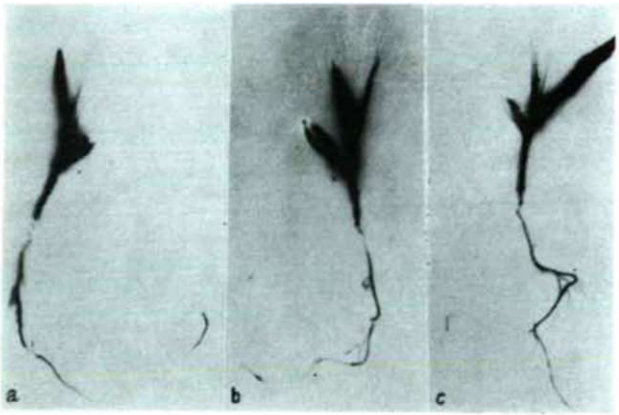

Fig. 2. Translocation of carboxyl-^{14}C-IAA in 12-day-old maize seedlings. Distribution of radioactivity in the plants (a) 2, (b) 6 and (c) 12 hours after treatment. Total activity on the third leaf: 0.5 μci per plant. The autoradiagrams were prepared on, "Forte Medifort R" film with an exposure time of one week.

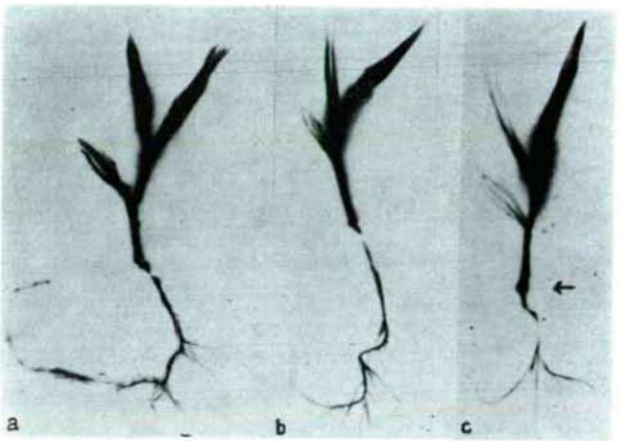

Fig. 3. Translocation of carboxyl-^{14}C-IAA in 12-day-old maize seedlings treated with butachlor. Distribution of radioactivity in the plants (a) 2, (b) 6 and (c) 12 hours after uptake. The butachlor and labelled IAA were added simultaneously to the culture solution. An extensive accumulation can be observed in the stem at the sites marked with arrows.

On the basis of the results it is concluded that butachlor slows down the basipetal transport of the exogenous IAA from the shoot towards the root; this may occur by means of direct inhibition, but it may also be the result of secondary processes.

Since one of the most important preconditions of the initiation of the adventitious roots (together with other factors) is a high concentration of IAA at the appropriate sites, it seems certain that the butachlor increases the possibility of the formation of adventitious roots by inhibiting the transport of IAA.

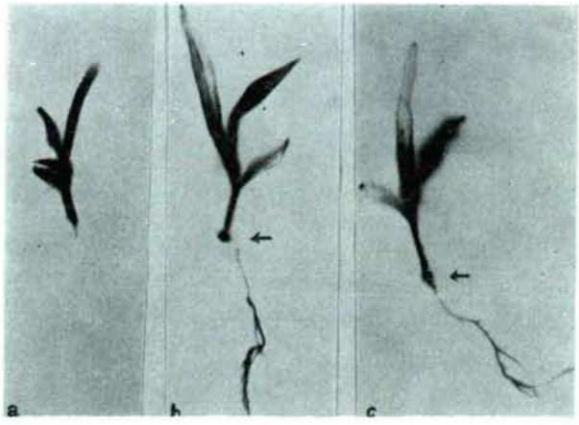

Fig. 4. Translocation of carboxyl-^{14}C-IAA in 12-day-old maize seedlings pretreated with butachlor-Distribution of radioactivity in the plants (a) 2, (b) 6 and (c) 12 hours after uptake. ^{14}C-IAA was transferred to the third leaf 24 hours after treatment with butachlor. Explanation as in Fig. 3.

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LIGHT- AND ELECTRON-MICROSCOPIC INVESTIGATIONS INTO THE CEROMA OF DUCKS WITH PARTICULAR REGARD TO THE HERBST CORPUSCLES

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Abstract

The ceroma consists of two layers, the external epidermis, and the internal corium. The epidermis is a stratified epithelium while the corium consists of connective tissue. The corium contains frequent mastocytes and there are several Schwanns' cells, Grandry and Herbst corpuscles.

In the Herbst corpuscle, three parts can be distinguished, the inner bulb, the inner cavity and the external capsule. The inner bulb consists of two cell layers each containing 8 to 10 cells. From cells 20 to 50 laminar processes come. The laminar system of any cell is connected with that of the cells before and after it, as well as with the similar system of the row on the other side.

In the axon running between the cell rows there are groups of mitochondria, dense core vesicles, clear vesicles, and neurotubuli. The axolemma is separated from the cytolemma by an easily discernible void gap. There is no synaptic organization along the membranes. The form of connection is a parallel contact.

The inner cavity consists of lamellae, bordered by fluidfilled cavities. The lamellae vary in shape and size and are characterized by long ribosome rows.

The extennal capsule consists of parallel lamellae, separated from each other by collagenous fibril bundles. The cytoplasm of the lamellae is sponge-like with, frequent oviform cistern.

Introduction

The structure and function of the afferent synapses have always particularly engaged the attention of those interested in the structure and function of the nervous system. As formations, resp. structures that inform the organism of the environment (peristasis) and its influence exerted upon the animal life, at first the epithelia came to the fore that entered into the service of the higher sensations by getting into a close contact with the nervous system in the organs of vision, audition, smelling and gustation. These were followed by those specialized in taking up mechanical stimuli, by getting into inner connection with the single nerve fibres. The possibilities for sensation grew more and more intensive and specialized when larger cell groups entered into communication by rising bundles of nerve fibres (Eimer's organ). A separate group is formed by the specialized epithelia that, jointly and severally each organized a nerve fibre connected to its terminal sector (Merkel's cell). The synaptic organs (Vater-Pacini, Herbst and Grandry corpuscles) developed as higher forms of accomodation. In these, connective-tissue sensory cells came into synaptic connection with sensory nerve fibres, developing around themselves laminar systems for increasing and ensuring the work of transferring the stimuli.

Materials and Methods

Our investigations were carried out on the piece of skin, the cere (ceroma) covering the maxilla of the domestic duck *(Anas boschas domestica)* and mallard *(Anas platyrhyncha)*. For the light-microscopic examinations there were used partly sections embedded in paraffin, and stained with haematein and eosin, partly frozen sections impregnated according to BIELSCHOWSKY—ÁBRAHÁM. The latter process proved to be very suitable for visualising the neural elements.

For electron-microscopic investigations, small pieces of ceroma were fixed in 0.5 p.c. osmic acid after being pre-fixed with glutaraldehyde. They were then dehydrated in the usual way and embedded in araldite. Sections were cut using a L.K.B. ultramicrotome and examined in a Jeol B.100 electron microscope. The investigations were performed in the electron-microscope laboratory in the Biophysics Institute of the Biological Research Centre of The Hungarian Academy of Sciences in Szeged. In the course of our work we were aided by Dr. FERENC JOÓ, leader of the laboratory, and Dr. IDA TÓTH and I should like to express my sincere appreciation to both of them.

Epidermis

The ceroma, as a typical vertebrate integument, consists of two parts. The external part is the epidermis, and the internal part, which is closely connected to it, is the corium. The epidermis is a stratified laminated epithelium, consisting of a deep inner layer *(stratum profundum)* resting on the corium, and a horny outer layer (stratum corneum). The deep layer consists of several cell rows. The upper of which is the granulous layer *(stratum granulosum)*. This is followed by the spinous layer *(stratum spinosum)* and then by the basic layer *(stratum basale)*. The cells of the granulous layer are full of round granules. Between cells, the intercellular ducts are obvious. The cells of the spinous layer are connected by the different protoplasmic processes and longer or shorter desmosomes. The nucleus is elongated, and segmented all round. The cells of the basic layer are partly elongated, and partly polyhedric. Between the cells, there are broad intercellular ducts, and the desmosomes are apparent. In the cytoplasm, the broad cisternae of the endoplasmatic reticulum are conspicoous, as well as canals and vesicles of the Golgi complexes. In addition to these, various vesicles appear in masses, or in a dispersed state. Ribosomes are arranged in rows along the cisternae of the endoplasmic reticulum, but there are also some free groups. In the horny layer *(stratum corneum)*, layers of flat, cornuous cells are arranged one above the other. The cells consist mostly of horny threads and a nucleus is rarely seen. The desmosomes are obvious. The horny layer, and the lower layers, contain much fat. During the treatment the fat is dissolved leaving round or elliptical cavities, arranged in a line or dispersed, full of fat *intra vitam*. This yellowish mass of fat gave this piece of skin the name cere *(ceroma)* (Fig. 1).

Corium

The corium consists of two layer. One of these is a loose layer *(stratum laxum corii)*, connected with the epidermis, while the other is a compact layer *(stratum compactum corii)*. The loose layer is comparatively thin and is composed of collagenous fibrils running undulately. It contains several connective-tissue cells. The cells are long tapering into long processes at each end. The nucleus is square and the chromatin consists of compact knots. This layer has no particular characteristic features. The compact layer is thicker, consisting mostly of collagenous fibres, and contains many connective-tissue cells, Schwann's cells, and nerve fibres. The connective-tissue cells are large and have processes. In their cytoplasm there are several Golgi comp-

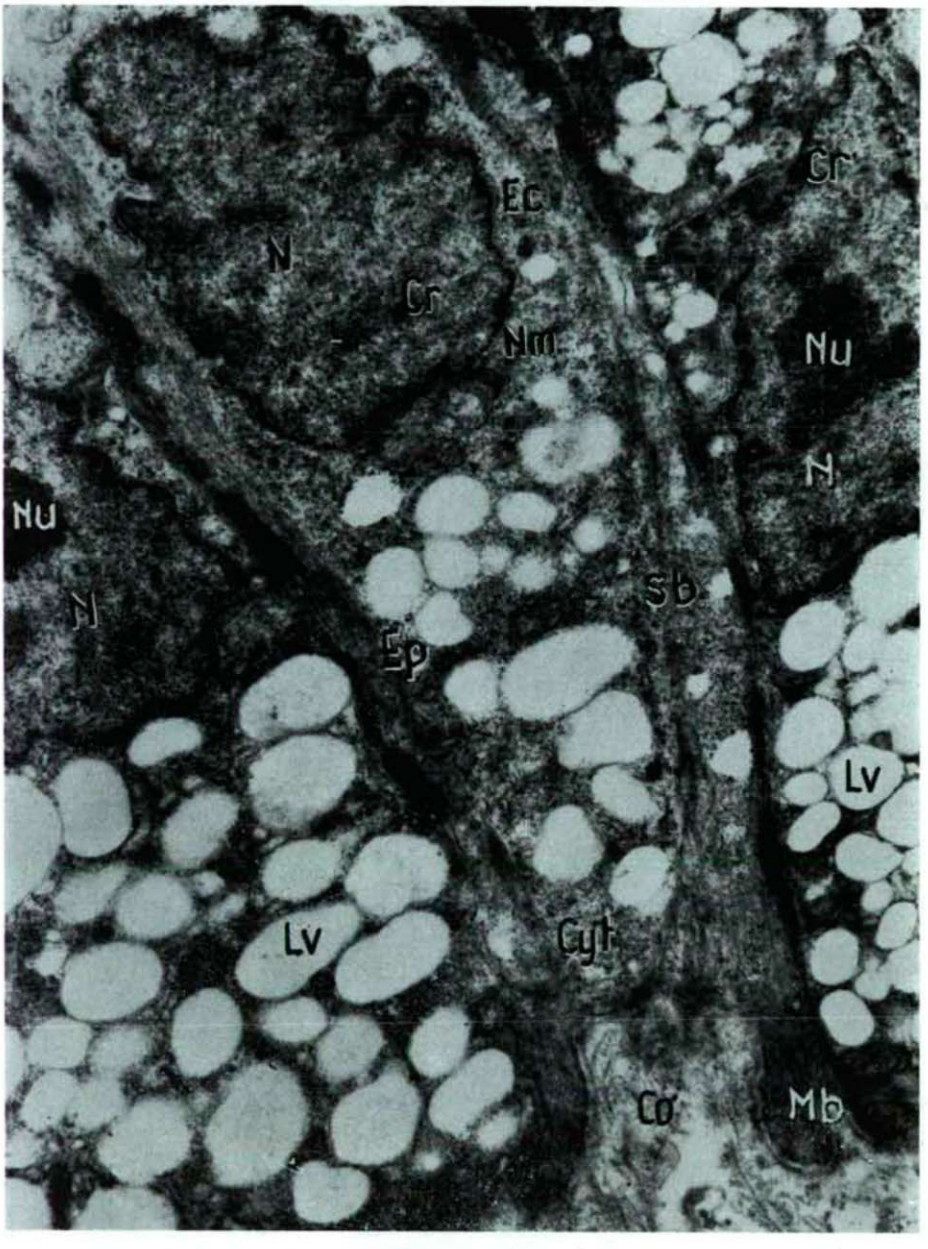

Fig. 1. Domestic duck *(Anas boschas domestica)* Ceroma. Ep = epidermis, Co = corium, Sb = stratum basale, Ec = epithelial cell, Cyt = cytoplasm, N = nucleus, Nu = nucleolus, Nm = nuclear membrane, Cr = chromatin, Lv = lipid-vesicle, Mb = membrana basalis. x16,000

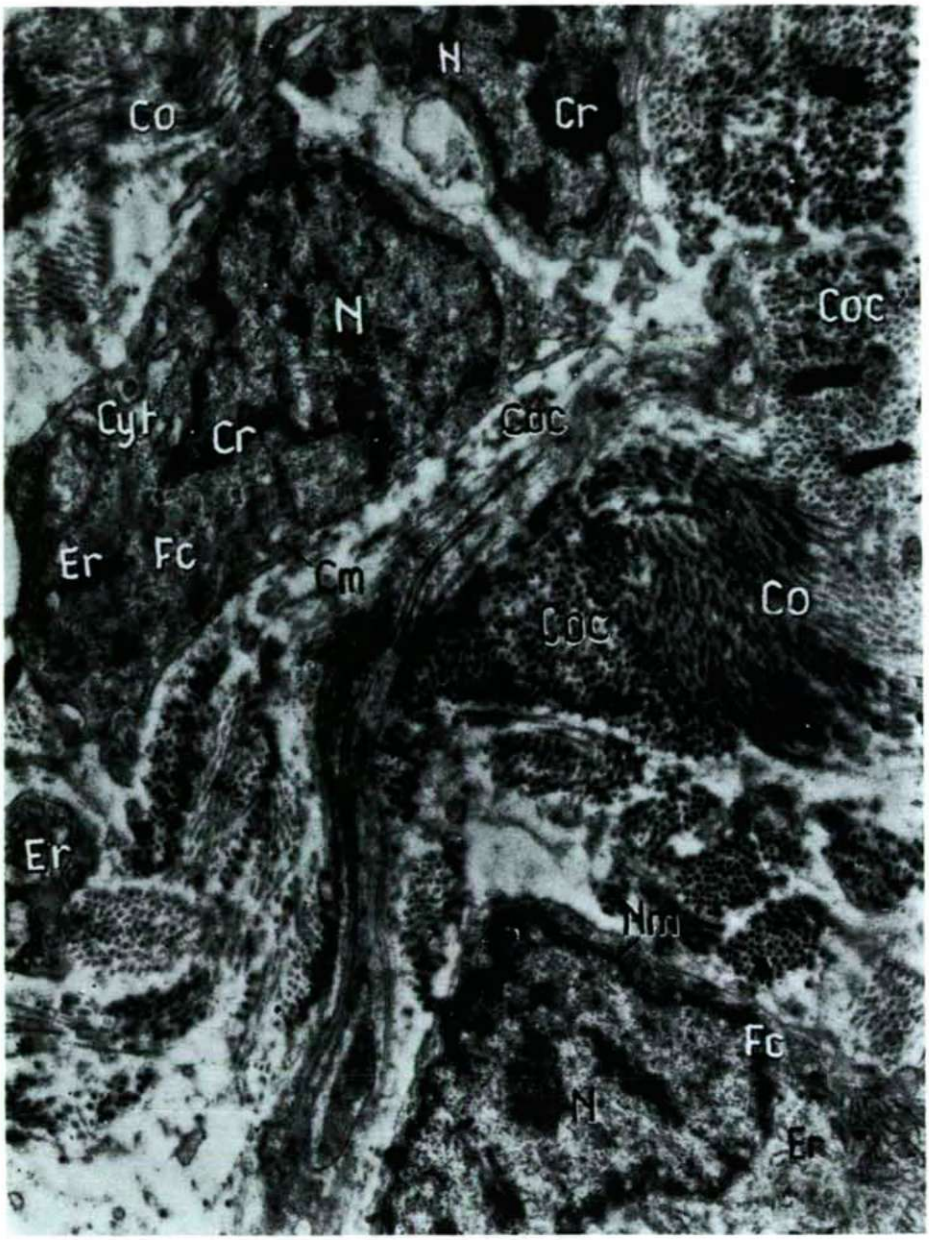

Fig. 2. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. Fc = fibrous-tissue cell, Cyt = cytoplasm, Cm = cell membrane, Nm = nuclear membrane, Cr = chromatin, Er = endoplasmic reticulum, Co = collagenous fibre in longitudinal section, Coc = collagenous fibre in cross-section. x16,500

lexes. The cisternae of the endoplasmic reticulum are broad. The shape of nuclei is highly variable. They may be segmented or polyhedric, and the square forms are also found. The chromatin is compact, and is concentrated directly below the membrane. A doubled membrane appears only rarely (Fig. 2).

Mastocytes

Mastocytes are rather frequent and are sharply discernible. They are not large, but elongated, sometimes segmented, cells. Their nucleus is round and contains knotty chromatin. The doubling of the membrane is obvious. The space between the two membranes is considerable, and occasionally widens out. The cytoplasm is full of round black-stained granules most of which there are empty homogeneous areas, of various sizes. Among the granules there are some which are full of smaller, uniform roundish granules. There are frequently some granule forms in the process of being discharged from granules, and others from which the contents have been fully discharged, transforming them into pale granules. These empty cells are generally named honeycomb (Fig. 3).

The most important characteristic of mastocytes, being studied by many people all over the world, is that, if excited, they discharge their metachromatic granules into the host tissue, the connective tissue (HIGGINBOTHOM, 1966). Some of the granules are taken up by the fibroblasts, but most of them go through a sudden lysis, losing histamine, their effective constituent. The mastocyte, which is an example of sequential exocytosis, resupplies its discharging granules. This has been verified experimentally (RÖHLICH, ANDERSON, UVNÄS, 1971).

In the metachromatic granules there is, in fact, an energy-demanding specific enzymatic mechanism (HÖGBERG, UVNÄS, 1957; UVNÄS and THON, 1961). This allowns the transport through the cell membrane of substances which can dissolve the biogenous amines of cells. Mastocytes are able to store, dissolve, and rebind the biogenous amines (RILEY, 1955). The process is cyclic, and has already begun in the embryo. "The ability of mast cells to discharge their metachromatic granules is their most striking histo-physiological feature and, presumably, the very basis of their biologic activity" (SELYE, 1965). It is generally supposed that the process resulting in the discharge of granules and the release of histamine, is a physiological mechanism, a response to the blood-supply requirements of tissues.

The granules of mastocytes were connected by some researchers (RHEINDORF, 1905; MEIROWSKY, 1908; JACOBI, 1912) with the granules of pigment cells. The electron microscope has provided a greater possibility to distinguish between the origin and development of these two kinds of granules. There are, nevertheless, some researchers even today who take a stand in favour of the common origin "the existence of common stem-cell". It is much more probable, however and is supported by electron-microscopic investigations, that the development of the two kinds of cells, and thus also of granules, occured in separate ways. This is also verified by the fact that we could not find any pigment cells in the ceroma of the domestic duck.

Mastocytes have been found in the various histological layers of the intestinal canal, in the respiratory tract, the serous membranes, and the lymph nodes (LEAHN, 1972). There are a great number of mastocytes in the corium, mainly in the vicinity of blood vessels, and often in close proximity to them. Some workers (ADAMS-RAY, 1959; ORFANOS, 1965; SZEKERES, 1974) found that mastocytes, and most likely the granules discharging from them are in close connection with the nerve fibres.

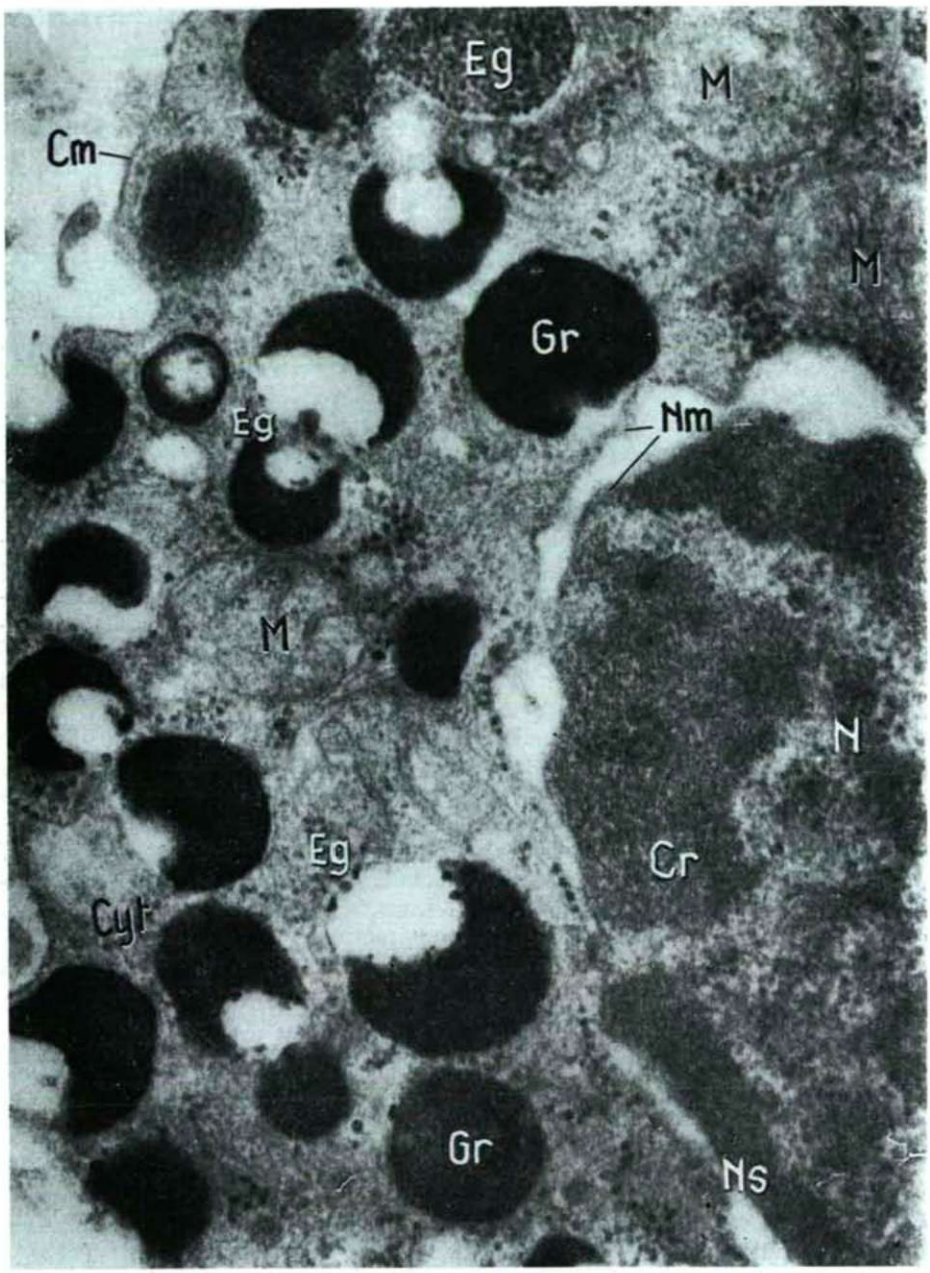

Fig. 3. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Mast cell. Cyt = cytoplasm, Gr = metachromatic granule, Eg = evacuating granule, N = nucleus, Nm = nuclear membrane, Ns = nuclear space, Cr = chromatin, Gm = cell membrane, M = mitochondrium. x260,000

Blood vessels

The capillaries are tubules of very narrow lumen. The lumen is fully filled with a single, nucleated erythrocyte. The endothelial cells are largely round with ovoid nuclei. Polymorphous nodules are formed by part of the chromatin. The erythrocytes are elongated elliptical corpuscles, strongly deformed, in the lumen of capillaries. The cytoplasm is strongly granular. Chromatin occurs along the nuclear membrane, in the form of a narrow stripe, in which broad nodules stretch towards the central part.

The postcapillary veins are tubules of characteristic structure. They appear in the microscopic pictures comparatively rarely. They are similar to capillaries but the lumen is wider and the endothelial cells are surrounded by pericytes. The endothelial cells are large and full of pinocytotic vesicles. Their nucleus is somewhat elongated but is, in fact, polymorphous. Between tha adjacent endothelial cells narrow canals are to be seen, running up to the border of epithelium. These serve for dilating the lumen. This phenomenon is almost exactly as described previously by us for the blood vessels of the human glomus caroticum (ÁBRAHÁM, 1970).

The long pericytes, curved, in accordance with their position, in sickle-form, are similarly full of pinocytotic vesicles. In addition to those described above, there is another feature, namely that the depressions between the protrusions of the endothelial cells are filled in by the protrusions coming from the body of the pericytes. This arrangement may similarly be connected with dilating the lumen and thus with the activity of blood vessels. The nucleus of the pericytes is extremely long, narrow and curved, its chromatin occurring overwhelmingly along the nuclear membrane (Fig. 4).

Nervous system

On the border of the loose and dense coria, resp. within the compact corium, a particularly large mass of neural elements can be found. Apart form the rich receptor system of the external genitals of Mammals, a region like this is hardly known where such an immense mass of neural elements can be seen. Immediately below the epidermis, arranged almost in a single line the Grandry corpuscles, and between, and below these, the Herbst corpuscles, are to be found in a large mass. This may of course, not be a definite regularity, but it should be emphasized that, in the cross-section, two to three Herbst corpuscles fall between any two Grandry corpuscles. To every Grandry corpuscle and every Herbst corpuscle a separate, easily seen nerve fibre is leading. This is, if impregnated successfully, sharply conspicuous. The course of these fibres can easily be followed on one or an other, nerve trunk which wary in thickness. It is, therefore, true to say that here is a real and very sensitive complex of sense organs which is characteristic of the ceroma (ÁBRAHÁM, 1976, Fig. 6).

What, from among the components of this complex, is the function of the Grandry corpuscles, and of the Herbst corpuscles, cannot be deduced without appropriate experiments. It can be supposed however even on the basis of morphological knowledge that the function of the Herbst corpuscles may be more general, these being characteristic generally of birds. They are limited to the ceroma, the mucosa of the oral cavity and the tongue and may serve the functions belonging to these areas. They are supposedly organs of the pressure sense. The Grandry corpuscles may serve a function belonging exclusively to the ceroma of ducks as bodies like these occur

Fig. 4. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Postcapillary vein. L = lumen, E = endothelial cell, P = perycite, N = nucleus, Ic = intercellular diverticulum, V = pinocytotic vesicle, G = Golgi complex, Cm = cell membrane, M = mitochondrium. x32,000

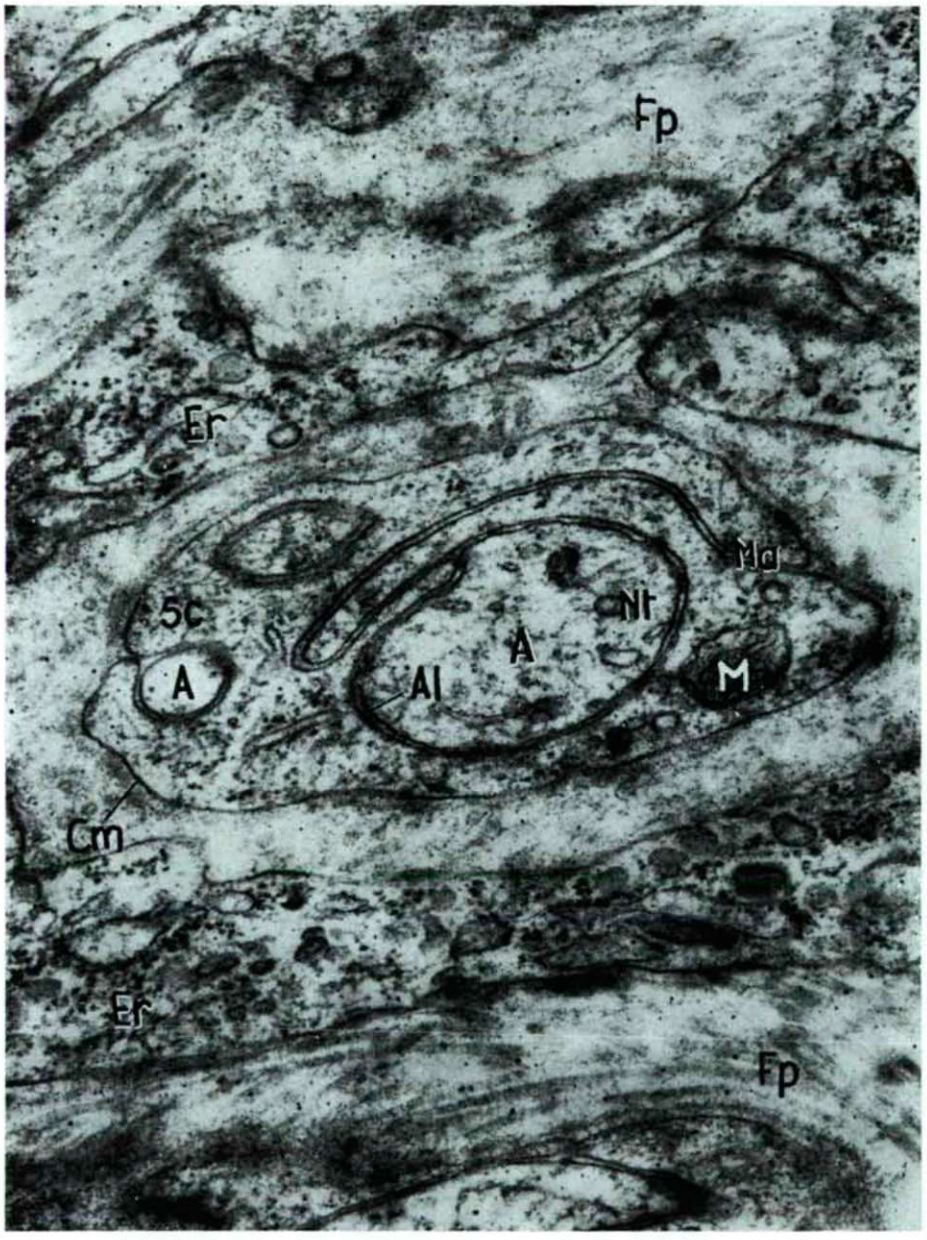

Fig. 5. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Sc = Schwann's cell, Cm = cytolemma, Ma = mesaxon, A = axon, Al = axolemma, M = mitochondrium, Er = endoplasmatic reticulum, Nt = neurotubules, Fp = fibrous tissue cell-process. x120,000

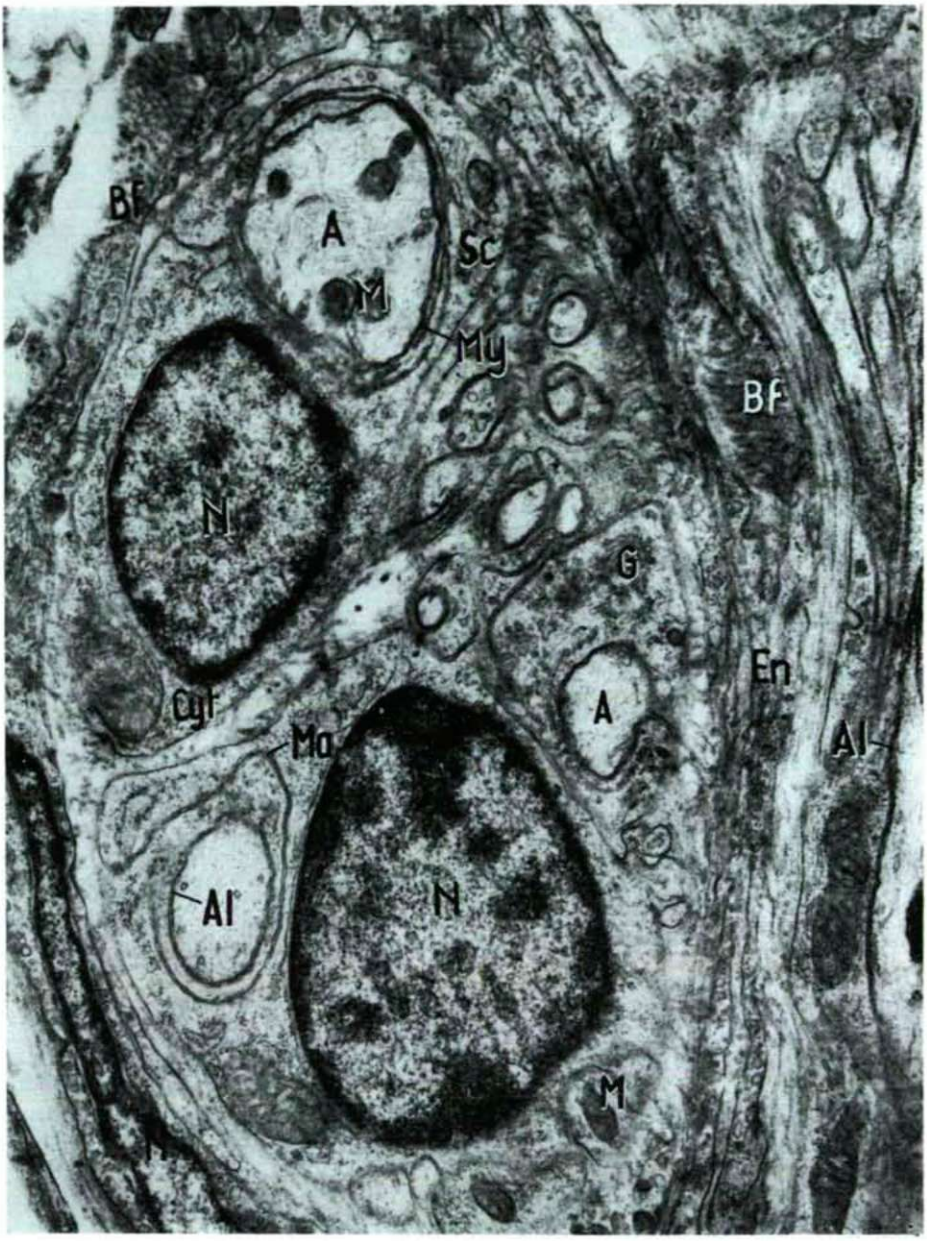

Fig. 6. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Sc = Schwann's cell, Cyt = cytoplasm, G = Golgi complex, N = nucleus, A = axon, Al = axolemma, En = endoneurium, Ma = mesaxon, My = myelin sheath primordium, M = mitochondrium.
x32,000

neither in other organs of ducks, nor in other birds. Or, if they yet occur, they do so only occasionally and in an extremely low number. They are probably organs of touch.

Taking into consideration that in the ceroma both endorgans are together, the question is raised as to what their combined function together and in such a large mass is. As the results of our investigations into Grandry's corpuscles have already been published (ÁBRAHÁM, 1976), we will deal below, apart from the general neural picture, with the structure of the Herbst corpuscles.

General neural picture

As to the general neural picture, the following can be said of it. There are particularly many Schwann's cells, most part of which are full of most forms of mesaxons. Among these are some penetrating only slightly into the cytoplasm, but others which protrude deeply into is (Fig. 5).

There are not infrequently canal systems, forming particular plexuses, ramifying in an extremely rich and complicated way. In the end-part of any canal, in a hemispherical sector, the cross-section of an axon in each of these can be seen well, and in this also the axolemma, within that the filaments, tubuli and in some cases mitochondria. Pictures like this occur in various sizes and forms. It is clearly shown by these systems how the axons are embedded more and more in the cytoplasm of Schwann's cells (ÁBRAHÁM, 1976, Fig. 7).

There are also some pictures, although rather few in which nearly all the phases of the formation of mesaxon are represented. In addition, it can also be seen, how the winding of the mesaxon round the axon-body, and with that the formation of the myelin sheath, begins. This process of winding is to be seen in the left upper corner of the next picture, above the nucleus (Fig. 6).

Further stages in the formation of the myelin sheath are clearly demonstrated in the next Figure in which the course of development of both membranes covering the nerve fibres can be followed exactly. The myelin sheath, already formed in Schwann's cell, the cytoplasm of the cell, its nucleus and nucleolus can be seen. There are also visible the forms of development following this, when the nucleus disappears and the cytoplasm shrinks. At last, the axon, and around it the myelin sheath and the neurilemma, which is a remnant of Schwann's cell-body, are to be seen. The axoplasm is clear and palely filamentous in any nerve fibre. The mitochondria in the axon are polyhedric, their number and situation is rather varied (Fig. 7).

It is clearly shown by the above pictures how the mesaxons are transformed as a result of the axial rotation into a myelin sheath and how Schwann's membrane developes from the remainder of Schwann's cell round the myelin sheath. It is interesting that while in Schwann's cell itself there are but comparatively few mitochondria, there occur — even if rarely — some Schwann membranes, that contain many mitochondria. These assemble in dense groups where they almost touch one another in certain parts of the membrane. On the other hand, in the other larger part of the membrane there can be seen no mitochondria at all (Fig. 8).

In Schwann's cells, apart from the axons, Golgi complexes can be seen in mass. In addition, there are a great many vesicles of changing size. Moreover, there are also ellipsoid bodies of thin wall, containing small corpuscles. The cisternae of the endoplasmic reticula are also visible, and beside these the ribosomes, arranged in a row.

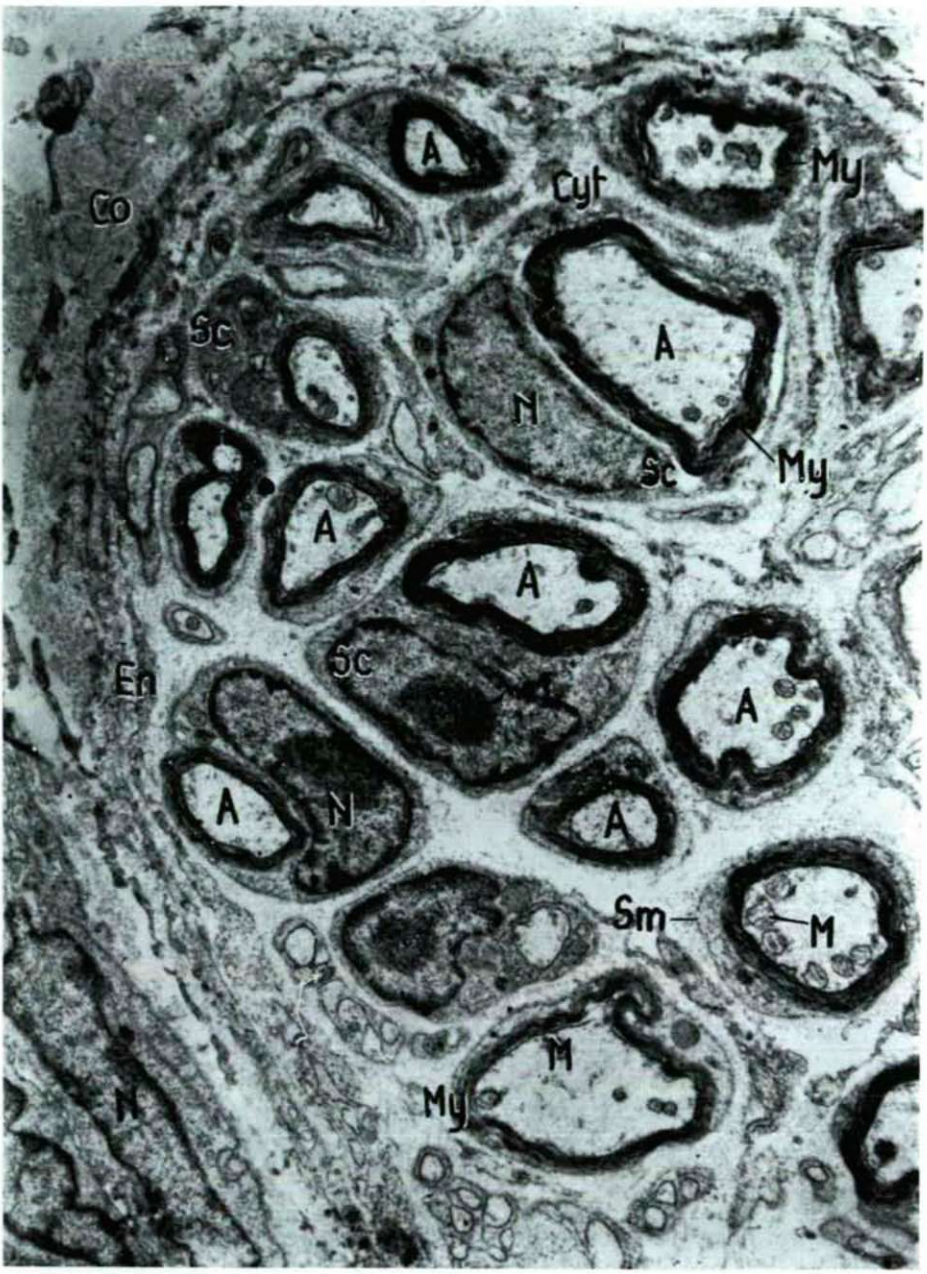

Fig. 7. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. Sc = Schwann's cell, Cyt = cytoplsm, N = nucleus, A = axon, My = myelin sheath, Sm = Schwann's membrane, M = mitochondrium, En = endoneurium, Co = collagenous fibre. x = 10,500

The Herbst corpuscle

The Herbst corpuscle was discovered by WILL in 1850. To study the structure of skin, he investigated the skin of the whole body of birds belonging to thirty different species. His aim was to see, how many Herbst corpuscles place on the single marked skin surfaces. He was also interested in the structure, and the differences between the Herbst corpuscle and the Vater—Pacini corpuscle occurring in the higher Vertebrates. To the latter question KÖLLIKER (1854) tried to give an answer.

The Herbst corpuscles were discussed, among others, by LEYDIG (1854, 1868), KRAUSE (1860, 1861), ENGELMANN (1863), HOYER (1864), RAUBER (1867), GOUJON (1869), GRANDRY (1869), IHLDER (1870), MERKEL (1875, 1880), KEY and RETZIUS (1876), HESSE (1878), KRAUSE (1881), LUDWIG FERDINAND von BAYERN (1884), SCHWALBE (1887), DOGIEL (1899, 1904). These authors generally say little about the structure of the endbody, having no procedures or means for approaching the fine structure.

Light-microscopic structure

The thorough description of the end-body is connected with the name of SZYMONOWICZ (1897) who established, on the basis of this studies, performed on the ceroma of the domestic duck, with methyleneblue, that the Herbst corpuscles are ovoid formations and are similar to the Vater-Pacinian corpuscles. MUNGER (1971) names the Herbst corpuscles the "cousins" of the Vater-Pacinian corpuscles. Their longitudinal diameter in the ceroma of the domestic duck varies between 120—160 μ. Their cross-diameter is 70 to 75 μ. The longitudianal diameter is parallel to the surface of skin. The endbody itself consists of two parts that is the central and the periferal part. The central part comprizes the axon, the plasmatic sheath, and the part formed by the tactile cells. The peripheral part consists of laminae, arranged concentrically round the central part.

The axon which is most essential component of the Herbst corpuscle, crosses the external laminar part surrounded by Schwann's membrane and the myelin sheath, and loses its myelin sheath in the internal region, Schwann's membrane reaches as far as the cells covering the plasmatic sheath.

The axon, entering the plasmatic sheath, becomes somewhat thicker and then, preserving this thickness, it runs along the longitudinal axis of the body. At the end, it thickens to a bulb form.

The axon, beginning from the place, where it loses the sheats, is surrounded by a homogeneous plasmatic sheath. Within this, it exists like a finger in a glove (SZIMONOWICZ, 1897).

Along the plasmatic sheath, at each of the borders facing each other on the right and left, there is a cell-row with 6 to 8 cells. The cells are flat and surround the axon in a continuous layer. The nuclei are large and ovoid.

The peripheral part consists of several concentric connective tissue laminae, among which there are few connective tissue cells. The endbody is bordered from outside by a connective tissue layer belonging to the corium, and surrounding the body like an envelope.

The laminae forming the peripheral part of the endbody are considered by

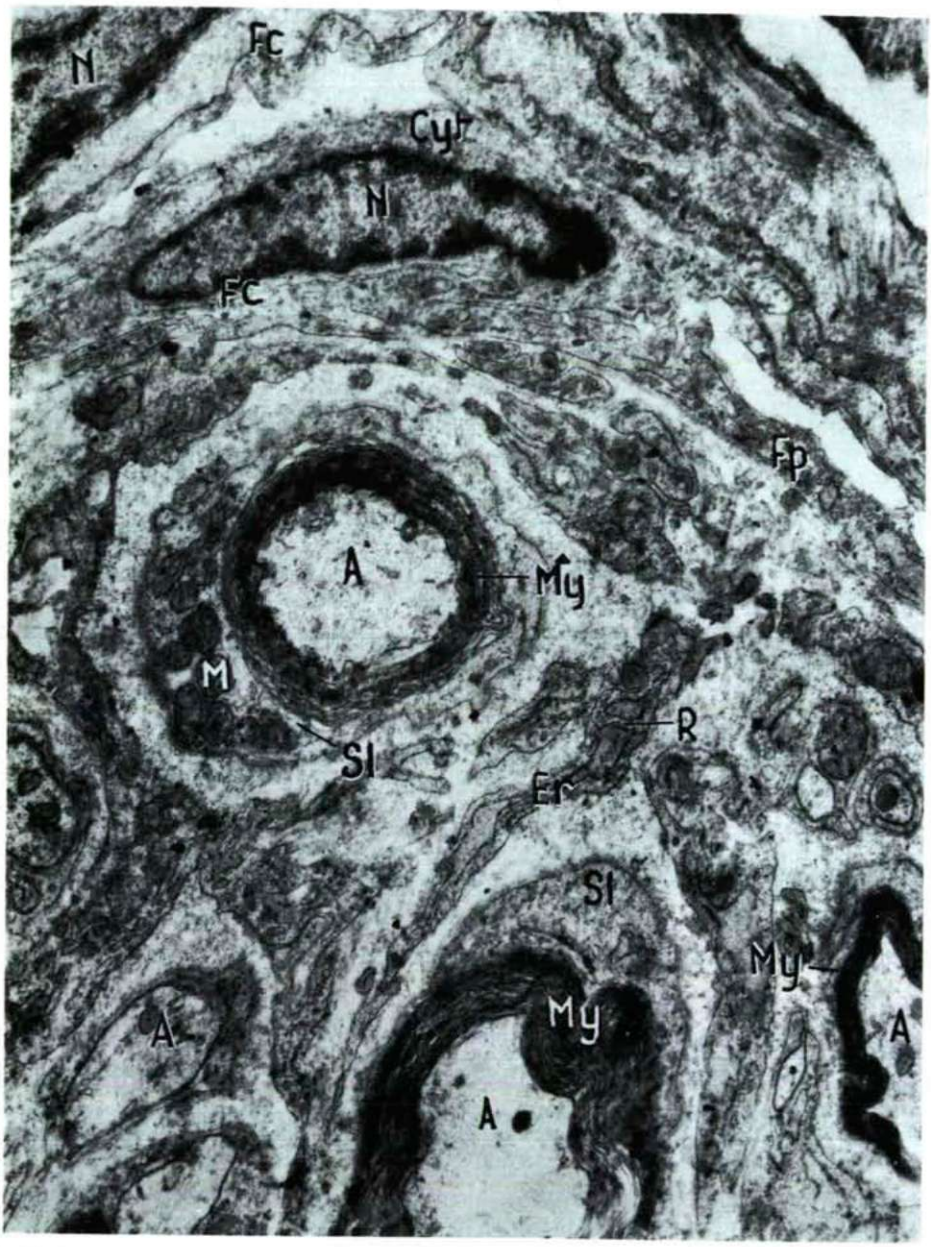

Fig. 8. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Cyt = cytolemma, N = nucleus, Er = endoplasmic reticulum, R = ribosome, Fp = fibrocyte process, A = axon, My = myelin sheath, Sl = Schwann's membrane, M = mitochondrium. x16,500

SCHUMACHER (1911) and CLARA (1922) as double membranes, enclosing fluid-filled cavities. The latter are, according to BOEKE (1934), kept open by an elastic fibre network. Publications by SZYMONOWICZ (1897) and DOGIEL (1899, 1904) concerning the structure of the Herbst corpuscles are, at any rate, generally confirmed by RUFFINI (1902) HERINGA (1917, 1920), CLARA (1925), and others.

MALINOWSKY (1967) investigated the ceroma of eight bird species, in addition to the skin of the mandible, the eyelid, the crest, the throat, the flap of outer ear, the feathered scalp, the skin of the cloaca-region, the mucosa of the oral cavity, the palate and tongue, in preparations impregnated according to BIELSCHOWSKY—GROS. He distinguished between three types of Herbst corpuscles found at the places investigated. For the classification he chose as parameters the relation between lengthy and breadth, number and form of nuclei, and the arrangement of the central part named inner bulb.

SAXOD (1973) distinguished three parts in the Herbst corpuscle on the basis of light microscopic investigations into the Peking duck, the white Leghorn chicken and the Japanese quail. One of these is the central part consisting of two cell-rows, and is called the inner bulb. The nuclei of cells occur on both sides, along the sensory nerve fibre running towards the axon. The second part is the inner cavity filled in by a system consisting of flat laminae supported by collagenous fibres. The third component is the external laminar sheath.

We could not identify these parts in our preparations stained with haematein and eosin. In our pictures not more than one part with nucleus and one with lamina could be distinguished, and even in these, the structure could not be recognized.

For clarifying the structure, a greater possibility was afforded by the silvered preparations made according to the procedure of BIELSCHOWSKY and ÁBRAHÁM. In these, the three parts named by SAXOD, namely the inner bulb, the inner cavity and the outer sheath can be recognized and delimited well towards one another although in respect to the details these remained in doubt in more than one respect.

In our silvered preparations, in the inner bulb the inner bulb cells, the inner bulb laminae, and the axon can be seen. But only the nuclei of the inner bulb cells are clearly visible. The cytoplasm presents itself in the form of pale and weak threads. One thing is extremely clear in this respect namely that the cells are in close connection, apparently in continuity with one another.

The laminar system of the inner bulb is striking but it cannot be established from this picture that the parallel laminae of the system originate from the inner bulb cells.

The axon, forming varices in the inner cavity begins from the inner bulb cells, becomes an increasingly thick homogeneous structure eventually assuming a bulb-like shape. In the sector of the axon falling in the region of the inner cavity, between two varices, on each sides, a large elliptical nucleus takes place. These are considered as the nuclei of wandering cells which have migrated here from among the inner bulb cells.

The inner cavity in the picture seems to be for most part homogeneous. There are to be seen occasional nucleus-like formations but it cannot be established whether these are nuclei or fragments of a lamina. It is, however, obvious that these fragments are in a concentric position and therefore can be qualified as laminae.

In the external laminar sheath the collageneous fibres are arranged in two or

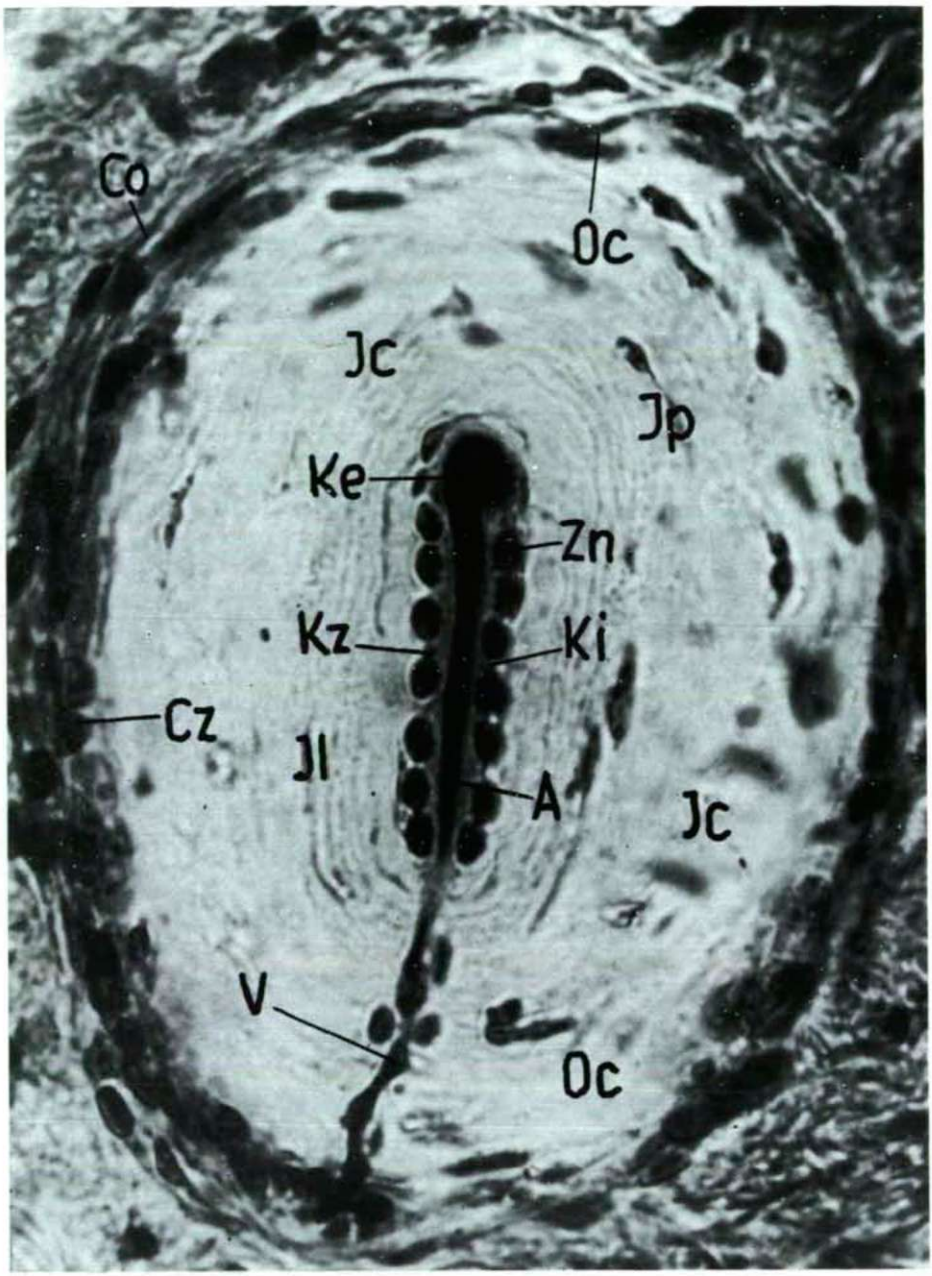

Fig. 9. Mallard *(Anas platyrhyncha)* Ceroma. The Herbst corpuscle. Ki = internal knob, Kz = internal knob cell, Zn = internal knob nucleus, A = axon, Il = internal knob lamina, Ic = internal cavity, Ip = internal-cavity plate, Oc = outer capsule, Co = connective-tissue fibre, Cz = connective-tissue cell, V = varix. Bielschowsky-Ábrahám's procedure. x1200

three rows and along these the connective tissue nuclei can easily be observed. Among them there are large elliptical forms which are almost identical with the nuclei of the inner bulb cells, and also elongated sharpened forms (Fig. 9).

Ultrastructure

In spite of the fact that many researchers have tried to recognize the structure of the laminar nerve endbodies, and among these that of the Herbst corpuscles, the endbodies have remained, in their entirely, unknown. The real structure was only discovered with the help of the electron microscope. This was a new world for everybody who was interested in the relations of end-connections in the nervous system and in the particular arrangements enabling the reception of stimuli in the sensory nerve fibres. It is natural that these investigations have started comparatively late since those enjoying the possibility of performing electron-microscopical investigations, were first of all interested in examining the central nervous system, and the higher brain activity. The electron-microscopic examination of the lamellated end-bodies and among these of the Herbst corpuscles, is essentially connected with the names of SAXOD (1969, 1970, 1973), GOGLIA (1969), NAFSTAD and ANDERSEN (1970), HALATA (1970), and GREGORY (1973). The results of investigations by these authors, are interesting and valuable but — as we read also in Saxod's comprehensive work (1973) — there remained still much to do, mainly in the domain of the neuron connection.

Cells of the inner bulb

The inner bulb consists of two cell rows. These cells are generally named sensory or signalizing cells (indicators). The nuclei of cells occur along the sensory nerve terminals, on both sides symmetrically. The number of cells was generally twenty in the species investigated. The cells are long bodies with processes, tapering at both ends. The nucleus is largely hemi-spherical, casually polyhedric and irregular, its margin towards the nerve fibre being hollowed out form a crescent-shape. The external surface of any cell touches some cell of the inner cavity. From its internal surface, 20 to 50 laminae originate. These taper ramifying or returning to the place of their origin. The laminar system of each cell is connected with the laminar system of any cell taking place before and behind it in line, as well as with the laminae of the cell row on the other side (Fig. 10). Thus in the photographs the picture of a laminar system suggests that is concentric in the cross-section of the body and parallel in its longitudial section. In the laminae, ribosomes and multivesicular bodies are frequent. Among the laminae, large ovoid vesicular groups appear here and there in pairs.

The nerve terminal

The Herbst corpuscle is innervated by a single myelinated fibre of trigeminal origin, forming several gyruses before entering the external sheath. It loses its myelin sheath and Schwann's membrane before entering the inner bulb. Throughout its further course it is a bare axon. SAXOD (1973) saw in it short spines and meandering processes but we have not observed any of these. The nerve fibre doubles in thick-

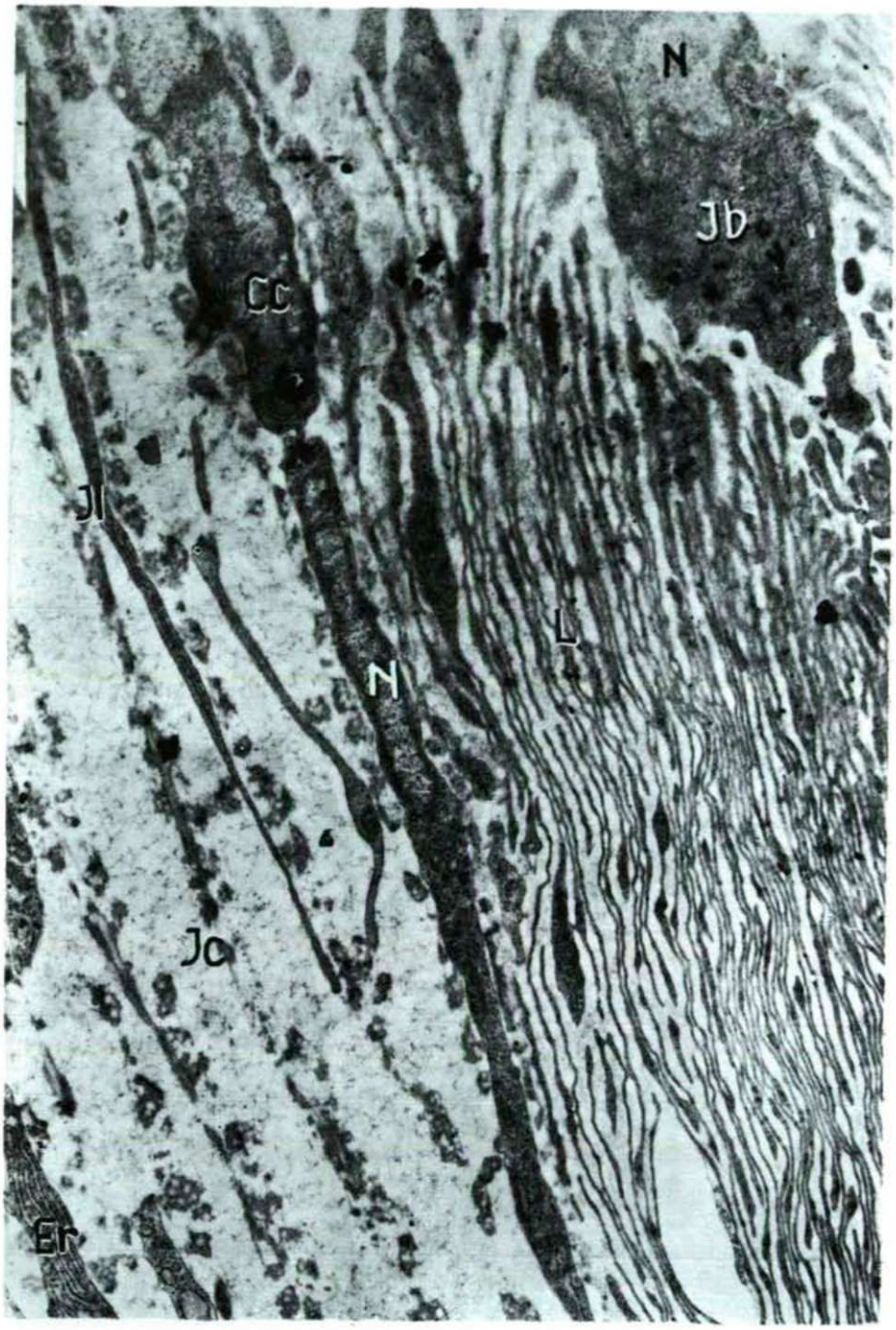

Fig. 10. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. The Herbst corpuscle. Ib = internal butt cell, N = nucleus, L = internal butt lamina, Ic = internal cavity, Cc = central cavity cell, Il = internal cavity lamina, Er = endoplasmatic reticulum. x16,500

ness at about the end of the body, and becomes ovoid, forming a neural terminal disk which grows first narrower and then broader.

The nerve fibre and, of course, the nerve terminal, too, are limited by the sharp homogeneous axolemma of equal thickness towards the cytolemma of the processes of the sensory cells. In the nerve fibre, and also in the nerve terminal, there are but few elongated mitochondria with crests, limited by a double membrane. The crests run lengthwise and each has a double wall. The walls are separated from one another by an obvious gap (Fig. 11).

In the axoplasm, in the terminal area, and in the nerve fibre itself, there are several roundish vesicles. Among these there are small forms with obvious lumens, larger empty forms, and also forms of dense core type, forming major groups. The last show a great similarity to the neurosecretory granules. In addition, we should point out the microvesicular bodies which are filled with vesicles of very different sizes. These include the elliptical organella enclosed with crinkled sheaths, containing roundish vesicles of different diameters. In the axoplasm, mainly in the vicinity of the end-disc, there are a great many neurotubuli, runing parallel with one another.

The axolemma is sharply delimited towards the cytolemma covering the laminae. The gap lying between them is obvious is of the same breadth in its entire course and thoroughly empty. There is no contact between the two membranes. No thickening can be seen on any of the membranes. The nerve ending itself is a splendid example of what the afferent synapsis consists of, and how the nerve fibre joins with the sensory cells supplying it with impulse conduction (Fig. 12). SAXOD (1973) found junctions of zolula occludens and zonula adherens type between the membranes covering the laminae and the axolemma. We have not found anything like this nor any of the nerve-like fibres, observed by NAFSTAD, ANDERSEN (1973) in the laminar system of sensory cells.

Taking into consideration that any sensory cell of the inner bulb has twenty of more processes, that several of these ramify, and that the laminar system of any cell is joined with the laminar system of the cells before and behind it, as well as to the laminar system on the other side of the nerve terminal, we have an idea of what an almost inexplicably complicated function system may exist even in a single sensory cell and how terribly sophisticated the mechanism starting the working process of the impulse conduction, ensuring its continuity, and furthering the stimulus to the nerve centres may be.

The internal cavity

The internal cavity consists of several laminae of varying breadth, separated from one another by a cavity system filled with fluid. The laminae are the cells of the internal cavities, standing with their processes in loose connection with one another. They are similar to the fibroblasts. Their processes enter the internal cavity, going round the inner bulb. There can be distinguished three groups of the lamina-shaped processes:

Those belonging to the first group are bodies of peculiar form and structure. They contain many voluminous endoplasmic reticula, delimited partly or wholly by a ring of ribosomes, as well as mitochondria of particular type, Golgi complexes, and here and there some vesicles. The characteristic ramifications and lateral out-

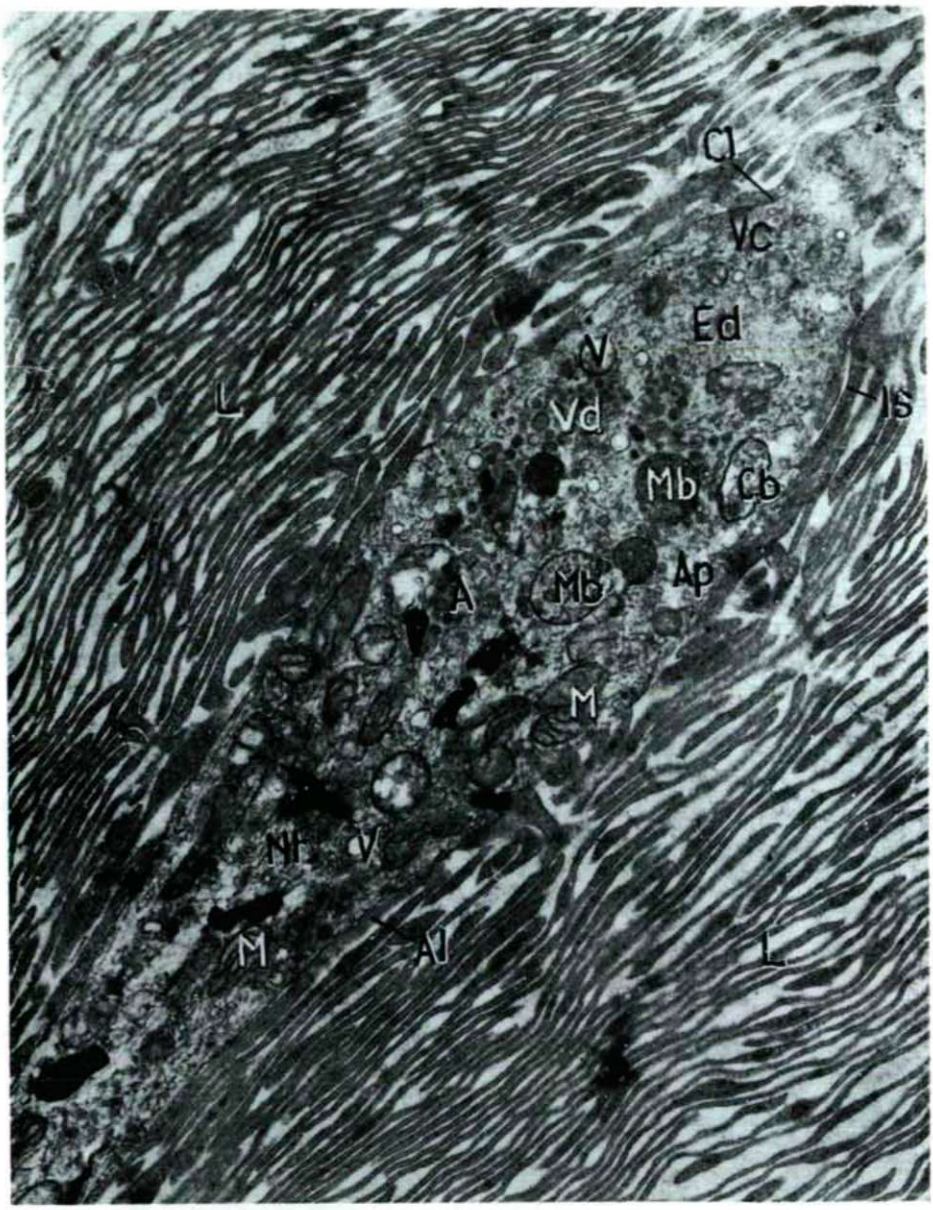

Fig. 11. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* The Herbst corpuscle. L = internal butt lamina, Mb = multivesicular body, Cl = cytolemma, Al = axolemma, Is = intersynaptic space, Ed = end disc, A = axon, Ap = axoplasm, M = mitochondrium, Nt = neurotubulus, Vd = dense core vesiculum, Cb = cylindrical body, Vc = clear vesicle, V = vesicle. x24,600

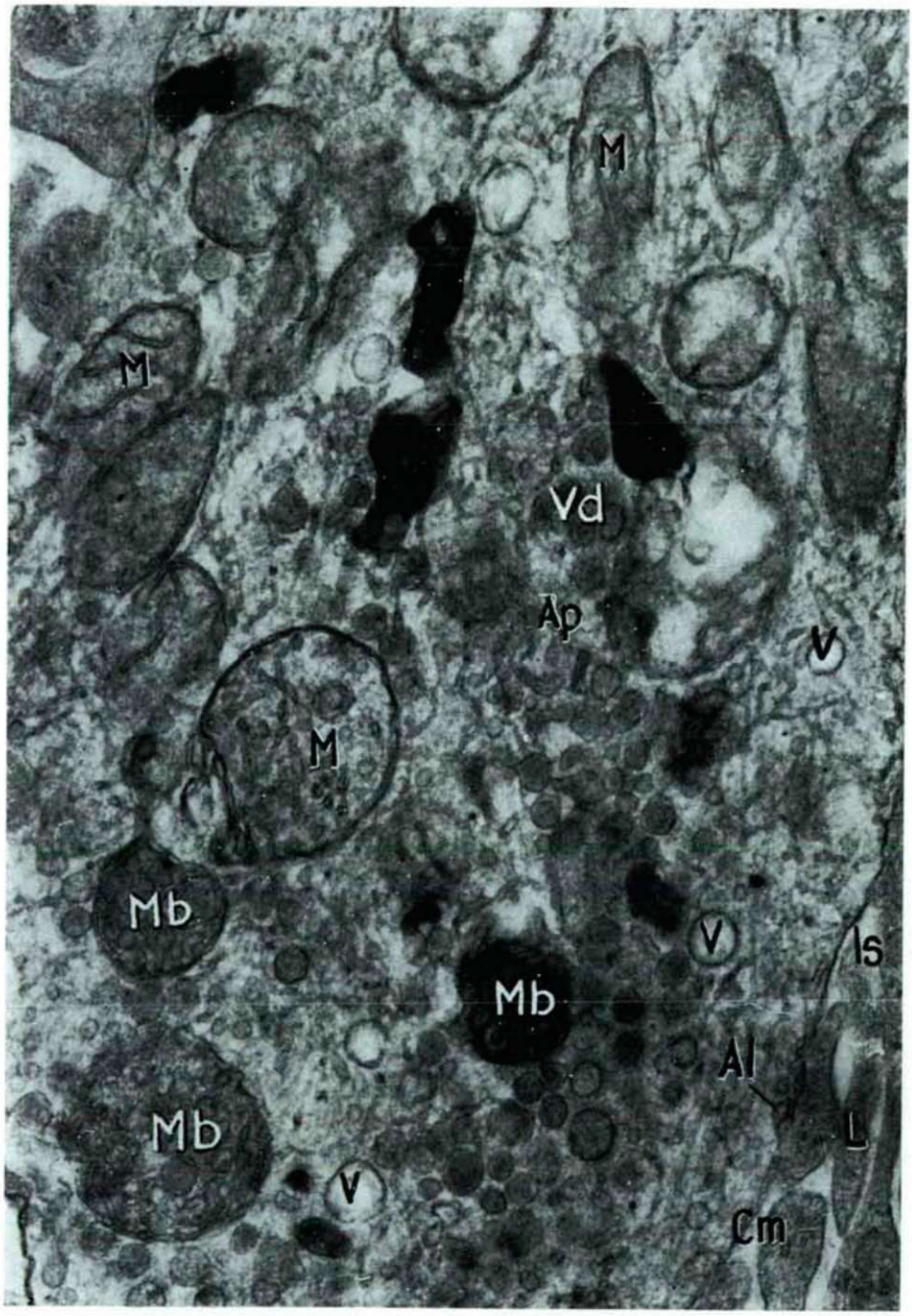

Fig. 12. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* The Herbst corpuscle. L = internal-butt lamina, Cm = cytolemma, Is = intersynaptic space. Al. = axolemma, Ap = axoplasm, Vd = dense core vesicle, Mb = multivesicular body, V = vesicle, M = mitochondrium. x85,000

Fig. 13. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* The Herbst corpuscle. L = internal-butt lamina, Lc = internal cavity lamina, M = mitochondrium, G = Golgi complex, V = vesicle, R = ribosome. x32,000

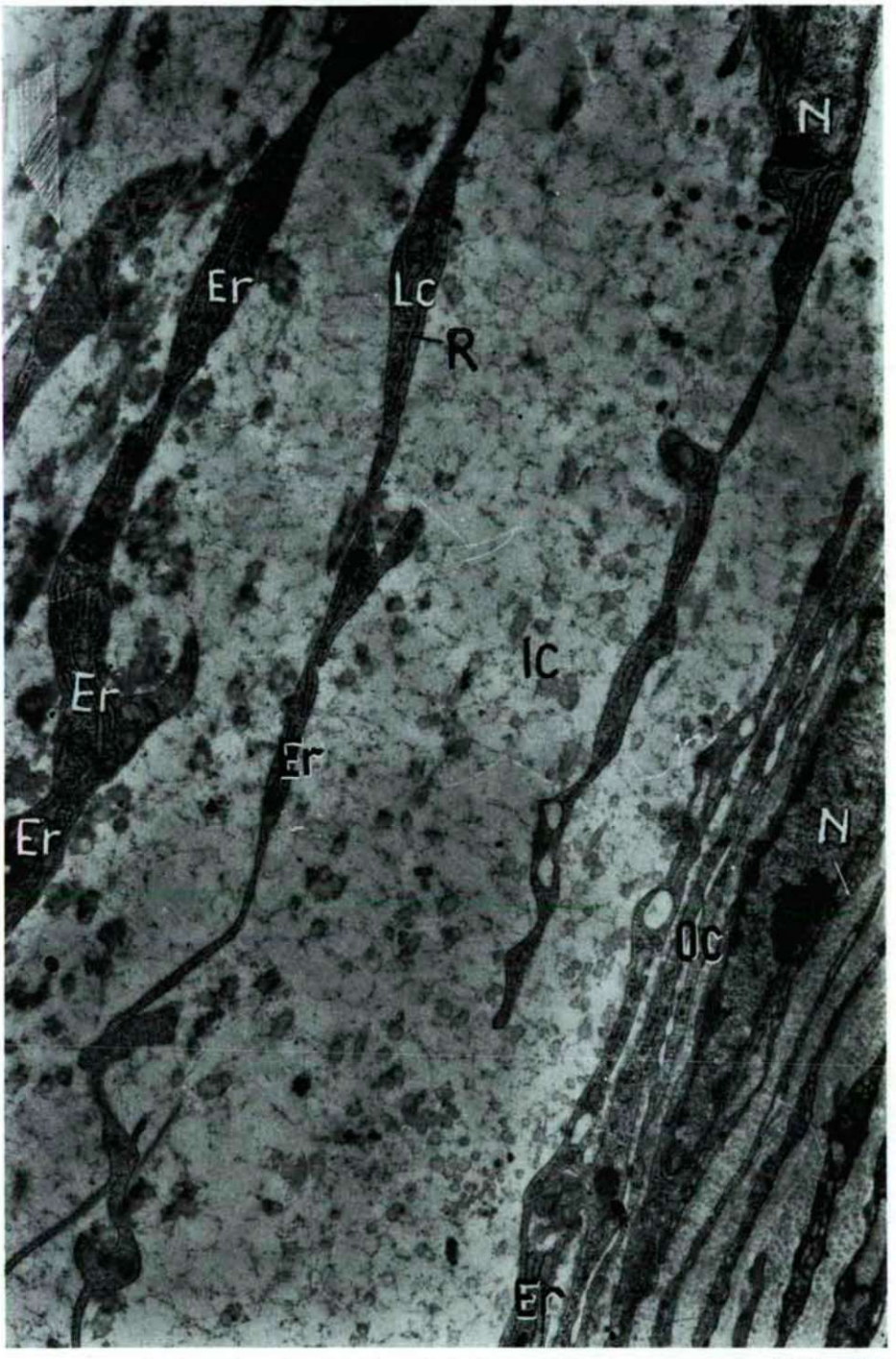

Fig. 14. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. The Herbst corpuscle. Ic = internal cavity, Lc = lamina of the cavity, Oc = outer capsule, Er = endoplasmic reticulum, R = ribosome, N = nucleus. x16,500

growths are frequent. In the empty space, multivesicular corpuscles are not infrequent (Fig. 13).

The laminae to be classified into the second group are bodies of straight course, ending in points. They are characterized by cisternae finding the way back and by ribosomes following the cisternae in a row.

The form of laminae to be classified into the third group is characterized by a nucleus rounded at one end and elongated at the other, with comparatively little chromatin. The cytoplasm is a very small, narrow strip on the nucleus, in other places it forms some knobs, repeated almost regularly. In the thin, initial sector of the lamina, the parallel running cisternae of the endoplasmic reticulum manifest themselves in the cytoplasm and the ribosomes form dense rows. A great number of rows of ribosomes are also to be found, which are not connected with the cisternae.

The external sheath

The external sheath of the domestic duck consists of 10 to 13 concentric laminae, separated from one another by collagenous fibrous bundles. The bundles run concentrically. Their thickness varies due to the volume of the cavities between the laminae. The number of the collagenous fibres greatly increases towards the stratum laxum corii. The laminae are comparatively narrow, but larger forms also appear, mainly in the middle part of the sheath. Their cytoplasm is sponge-like, containing several empty vesicles of different forms and sizes. Some of the laminae ramify. There are also a very few which have two nuclei. The nuclei are long, one end being obtuse, and the other sharpened. The nuclear membrane is well-defined. Part of chromatin is joined with the nuclear membrane while the remainder appears in the form of tiny granules (Fig. 14).

The laminar system, occuring in the stratum compactum, is delimited by the loose fibrous system of the stratum laxum corii and by a large mass of the characteristic fibroblasts.

Discussion

There is hardly any detail of the nervous system in which the research workers of different ages would have been so interested as the sensory fibres and the sensory terminal apparatuses which in the organs of surface position, primarily in the common integument, single or covered with different membranes, serve for receiving and conducting impulses originating from the environment. We should have to gave quite a long list of prominent and devoted researchers even if we wanted to enumerate only the names of those trying to recognize the structure of receptor apparatuses falling to the region of the common integument, and trying on this basis to draw conclusions concerning their activity.

The series of problems — the components of which were discovered and discussed with the help of the methods and means available at the different times — was always to recognize the following: Where are the sites where the sensory nerve fibres and receptors are situated, what are the tissue groupings which surround the nerve fibres and nerve terminals respectively, connecting these with the environment, and lastly, are there in the nerve fibre any organelles by means of which they respond to the effects of the environment with a particular sensitivity?

Most of the problems had already been solved by the middle of the Nineteenth

Century using light- microscopy, but there remained many questions which could only be solved with the electron microscope. This latter has opened in many areas and several respects quite a new world for the researchers interested. The electron microscope has revealed the laminar systems surrounding the nerve fibres, and the nerve fibre itself. Some problems have remained, all the same, requiring other devices and conceptions before they can be solved.

The problems of the laminae of Herbst's, Vater-Pacini's and Grandry's endbodies — which under a light-microscope did not appear clear at all — now seem to be solved. The structure of the sensory cells formed into a line in the central part of the Herbst corpuscles came to light, and from this the form of connection of the laminar system of the inner bulb with the nerve fibre also became clear. The laminar system of the inner cavity and external sheath was, correctly interpreted.

The electron-microscope pictures, illustrating the structure of the Vater-Pacinian laminar system, justified the separation of the external and internal sheaths. At the same time they showed how much the cells forming the laminar system of the Pacinian corpuscles differ from the sensory cells and laminar system of the Herbst corpuscle (CHOUCHKOV, 1971). Although in the structure of the sheath, and in the connection of the sensory cells and satellite cells there is some similarity, the covering, enclosing the sensory fibre in the Grandry corpuscle shows quite another picture.

The electron microscope has presented a different picture to the world, concerning the position of the nerve fibre runing along the endbodies. The bare axon of the Herbst corpuscle, preserving its original thickness, runs through the middle of the inner bulb up to the third-fourth part of the endbody. Here, close to the end, it widens, then narrows and, finally, ends rounded as a bulb. DOGIEL (1899) and SAXOD (1973) found tiny protrusions and processes on it. We have not observed anything like these and found the axolemma smooth, homogeneous and of equal thickness throughout its whole length. The gap between the axolemma and cytolemma is spacious and constant. SAXOD (1973) found some homogeneous granular substance in it but we have not seen anything of this type.

The axon of Pacinian endbody contains dispersed mitochondria, neurofilaments, and neurotubuli. Its ending is sometimes double, occuring at the pole of the endbody, between the internal and external sheath (CHOUCHKOV, 1971). In some regions of the axolemma some desmosome-like formations were observed, but synaptic formations were not found. In the bare axons running through the Grandry corpuscles with a single sensory cell, the mitochondria form a chain. On the other hand, in the endbody with two sensory cells, starting from the site of ramification mitochondria are entirely missing (ÁBRAHÁM, 1976).

In the nerve terminals of the Herbst corpuscle there are many mitochondria, situated round the neurotubuli. There are several vesicles of synaptic-vesicle type. The number of dense core vesicles is much smaller (SAXOD, 1973). According to our investigations, there are few mitochondria but many roundish vesicles. Among these there are some smaller ones, with an empty lumen delimited by a sharp membrane, and also larger forms of dense core type. The latter form groups and show a great similarity to the neurosecretory granules. There are some round bodies delimited by a sharp wall, full of vesicles of different sizes. There are also some particular elliptical bodies enclosed by a sheath, containing some vesicles of different diameters, and there are several neurotubuli parallel in position.

CHOUCHKOV (1971) found some axoplasmatic protrusions in the broadened endbulb of the central nerve fibre of the Pacinian corpuscles. These consist of neurofilaments with varying position and form. Some of them are elongated others are cone-shaped, and the remainder are rounded. They are situated between the collagenous fibrils at an equal distance from one another, being connected together chainlike. In the protrusions there are no mitochondria, endoplasmic reticulum, or lysosomes. But at the point where the protrusions begin, the mitochondria form a dense mass.

In the axoplasm of the terminal ramuli of the Grandry corpuscles with double sensory cells, there are also neurofilaments, synaptic vesicles, and granular vesicles (ÁBRAHÁM, 1976). SAXOD (1973) observed various juction-forms between the sensory cell and the nerve terminal. We have not seen any junctions. According to our investigations, the space between the membranes is completely empty. We consider the connection as a typical parallel contact.

In the axoplasm of the Grandry corpuscles with one sensory cell, and in the area of the sensory disc, there are so many mitochondria that they are almost in contact with one another. Immediately under the axolemma, vesicles of synaptic type and microvesicular corpuscles are also to be seen. The axolemma is sharp and homogeneous, and both of its margins are smooth. The cytolemma is well-delimited, and the gap between the membranes is obvious, spacious, empty, and of equal diameter through its entire course. The connection between the two membranes is qualified as a parallel contact. We have seen a thickening only once in the axolemma and opposite to it, in the cytolemma, near to its end. It is difficult to decide whether this is — is spite of the fact that below the thickening in the axolemma synaptic vesicles exist — a synapsis or a desmosome *(zonula adherens)*, but as there is no grouping of synaptic vesicles on either side, we consider the form of junction as a desmosome.

ANDERSEN and NAFSTAD (1968), and NAFSTAD and ANDERSEN (1970) saw two nerve fibres in the Herbst corpuscle. One of these was the central afferent fibre, while the other was found in the laminar system of the inner bulb and qualified as an efferent fibre. In the Pacinian corpuscle, the same situation was found by CHOUCHKOV (1971) who similarly speaks of afferent and efferent fibres. He found the efferent fibres between the external and internal sheaths.

The problem is not new. It has already been observed by more than one worker that the receptors contain both afferent and efferent synapses. From among those doing pioneering work in this area, the names of SMITH (1956), WERSÄLL (1956, 1961), BAIRATI (1961), ENGSTRÖM (1961), JURATO (1962), FLOCK, KIMURA LUNDQUIST and WERSÄLL (1962), and SMITH and RASMUSSEN (1965), are to be mentioned. It became known following their activity that in the vestibular epithelium of the higher Vertebrates, sensory cells of two different types can be found. These were designated as hair cells of first and second type. This was followed by the discovery that the hair cells of first type were entirely surrounded by the centripetal nerve fibre the scarcely granulated calix and the hair cells of second type were supplied with two different nerve terminals of different structure, in sharp contrast to each other. One of these is scarcely granulated, being in synaptic contact with the membrane of the sensory cell. This ending — judged by its structure — is postsynaptic. The other ending which appears in lower number is circular and densely granulated (ENGSTRÖM, ADES, HAWKINS, 1965). It is in contact with the surface of the sensory cell and, in the region of contact, a distinct thickening is visible both in the plasma-

membrane and in the axolemma. This synapsis form is qualified as efferent. The mammalian vestibular epithelium has double innervation verified by JURATO (1962) who observed, after the olivocochlear bundle being transect, some synaptic elements of the cochlear receptors degenerate.

Similar problems were dealt with by HAMA (1969) who — in the course of his investigations into the auditory spot *(macula acustica)* of the goldfish *(Carassius auratus)* — found two forms of connection between receptor cells, and of nerve terminals. In one of these, the electron density of both the nerve terminal and the membrane of the receptor cell is increased. The electron dense material is mainly stored in large amounts in the axolemma. In the sensory cell, the accumulation is slighter. In the receptor cell, near the plasma-membrane, a roundish electron dense body can be observed, bordered by a layer consisting of vesicles.

In the second form of connection, there aren't any specializations, either in the plasma-membrane of the receptor cell, or in the axolemma, which are generally characteristic of synapses. Here the two synaptic membranes shut each other, and the nerve terminal is full of synaptic vesicles, some of which are open towards the intersynaptic space. Among the synaptic vesicles there are also a few dense core vesicles.

Concerning the activity of the two synapsis-forms, HAMA, has the following — in our opinion right — ideas. The first synapsis-form, where the groups of synaptic vesicles are in the receptor cell and the thickening is more obvious on the side of the nerve terminal than on the side of the receptor cell, it is an afferent synapsis in which the stimulus is transferred from the receptor cell to the nerve terminal. In the second synapsis-form, the vesicle groups take place in the nerve terminal. Consequently, the direction of impulse transfer is from the nerve terminal to the plasm of the sensory cell. The contact qualifies, therefore, as an efferent synapsis. In respect of functioning it is named inhibitor.

ÁBRAHÁM (1968, 1969, 1970a, b) described from the human glomus caroticum some synapses, clearly showing every feature of the efferent synapses. Taking into consideration that the glomus caroticum is a chemoreceptor, as verified structurally and functionally, the question is raised, as to what is the function of the efferent synapsis. It is however generally, and unanswered question what role the efferent synapses in the receptors play. They may be inhibitors or moderators but they may in addition, serve another function. At any rate, as we cannot give a generally acceptable reply to this question, we are also at fault for drawing an uniform picture of the structure of the peripheral sensory nerve terminals, of junctions, and of the general structure of the afferent synapses.

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PRELIMINARY STUDIES ON THORACIC GANGLION-CELLS OF MAY-FLY LARVA (PALINGENIA LONGICAUDA OLIV., EPHEMEROPTERA)

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Abstract

The thoracal ganglion cells of the may-flay larva are studied, and the paracrystalline bodies and the cytosomes with different structures are described. Both of these originate from the mitochondria, or more exactly the paracrystalline bodies from the mitochondria and the cytosomes themselves from the crystalline bodies. It is considered possible that these play a part in the matter-energy transport of the cell.

Introduction

Apart from the generally-known cell organelles, we are aware of more and more organelles that occur only in a few sorts of cells and only under certain conditions. The structures, origin and particularly the activities of the latter have from many points of view not been clarified.

Of late, investigations into transforming mitochondria (ÁBRAHÁM, 1972; KUCERNROWICS, 1953) or, e.g. cytosomes have been coming more and more into prominence. The latter were particularly investigated in the case of molluscs (Mollusca), in connection with problems of the generation and storage of energy (CHALAZONITIS et al., 1968; LACY et al., 1956; NOLTE et al., 1965;ZS. -NAGY, 1967; 1969).

The aim of the present paper is to give an account of the structure of special organelles found in the thoracic ganglion-cells of may-fly larva, and their possible activity in the cell. These organelles can be compared well with the cytosomes described for molluscs (Mollusca).

Materials and Methods

Our investigations were performed on the thoracic ganglia of may-fly larva (*Palingenia longicauda* OLIV.) at different developmental stages. After Bouin and Carnoy fixing some of the ganglia were stained with haematein-eosin, or chromhaematoxylin-floxin, corresponding to the aims of the light-microscopic investigations, while for electron-microscopic investigations the fresh matter (immediately after being collected)was fixed in a pre-fixing mixture with glutaraldehyde (KARNOVSKY, 1965) and then in buffered osmium tetroxide (pH 7,2—7,4). Semi-thin sections were contrasted with toluidine-blue, and ultra-thin ones according to REYNOLDS' method (1963). Micrographs were made with a TESLA BS-500 electron microscope.

Result and discussion

In each of the three thoracic segments of may-fly larva one pair of ganglia is situated. The last of these (ggl. metathoracale) is a ganglion complex (CSOKNYA et al., 1977).

All the nerve cells comprising the ganglia are peripheral in position. According to their size, they are either large (giant) (180 μ) or small (40 μ) cells. In both cells, we could observe granules that could be stained strongly with the staining procedures applied. Besides the even granulation of the cytoplasm it is obvious that the large cells contained "empty" vacuoles in almost every case; these were mostly to be observed on the side opposite to the axon. The cytoplasm of nerve cells showed a similar picture in any larval stage.

After studying our electron-micrographs, we could establish that in the perikaryons of nerve cells there are particularly many mitochondria and dense-bodies of very varied appearance and structure. The latter, on the basis of their structures are not uniform. All transitory forms can be recognized from the forms with an almost regular, "crystalline arrangement" to those containing a loose membrane system (pictures in Plates I, II, III, IV and V).

Most characteristic are the solitary paracrystalline bodies (Plate I, Figs. 1—2), with a size of 1.6—1.7 μ on the average, but even larger ones can sometimes be observed. It is characteristic of their structure that they are limited from outside by a unitary membrane, and in their interior strongly dense membranes are stratified upon one another, at a distance of 100 Å (CSOKNYA et al., 1976).

We may often observe their arrangement in groups as well (Plate I, Fig. 3), where the fusion of the single paracrystalline bodies in only rarely to be seen. These locally grouped bodies gradually loose their regular internal arrangement, and granules of changing size and density appear in them. This phenomenon can also be observed in the case of solitary bodies.

This structural loosening is the beginning of a process leading to the complete transformation of the bodies. Such states in transformation are shown by the pictures of Plates II, III and IV. At the end of the process (in our opinion) the bodies become empty and these forms evacuated in groups may have corresponded to the vacuoles observable by light-microscope.

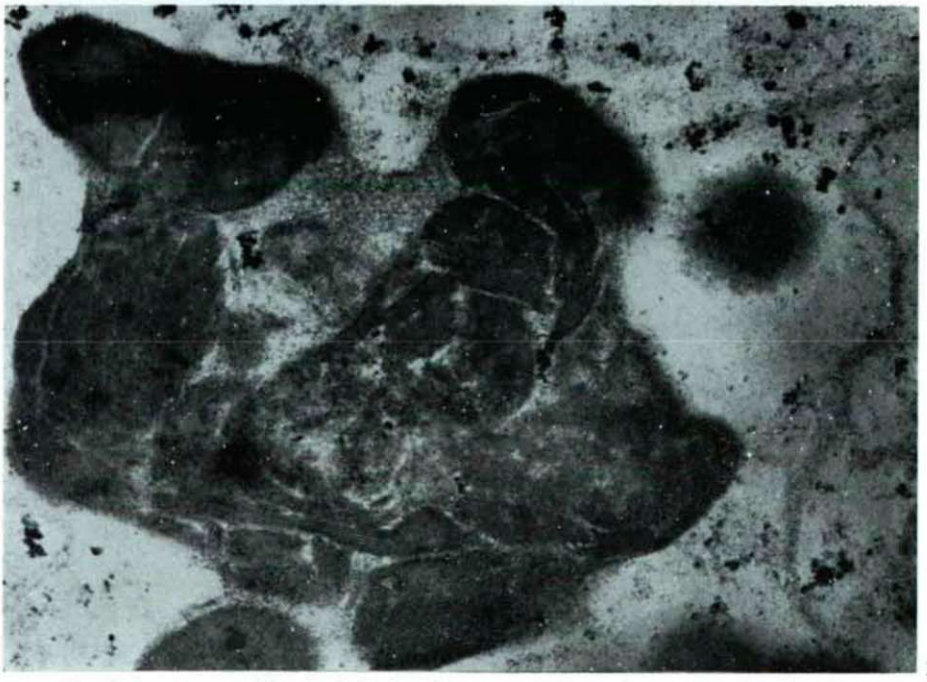
In their varied appearance and structural building-up, these organelles show considerable conformity with the characteristic bodies described from the central nervous systems of shell-fishes and snails, the cytosomes (CHALAZONITIS et al., 1968; FÄHRMANN, 1961; LACY et al., 1958; ZS.-NAGY, 1967). Because of their respiratory-enzyme content, these cell organelles are sharply differentiated from the lysosomes, but a genetic connection is assumed between them and the mitochondria (FÄHRMANN, 1961; NOLTE et al., 1965; ZS.-NAGY, 1969). We, too, want to confirm this latter fact with our morphological observations. A part of the mitochondria of the ganglion-cells exhibit a regular structural building-up, while in others the internal lamellar system is much richer, the membranes are arranged close to each other and, simultaneously with this, their density strongly changes (Plate V, Figs. 1, 2 and 3).

On the basis of our electron-microscopical experiences, we see that these bodies

Plate I

1

2



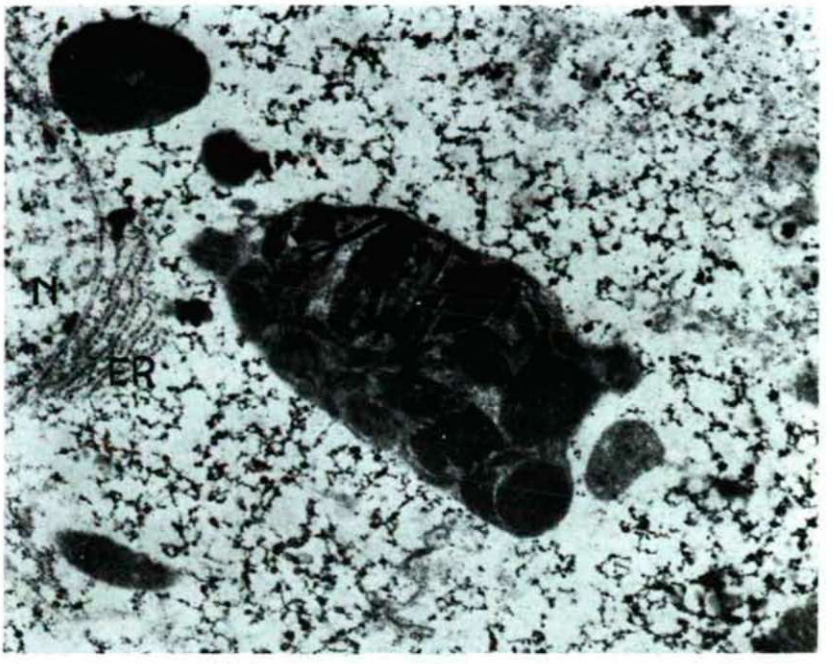
3

Fig. 1. A paracrystalline body limited by an endoplasmatic reticulum (ER- endoplasmatic reticulum). x48 000
Fig. 2. Solitary crystalline body. x48 000.
Fig. 3. Accumulated paracrystalline bodies. x36 000.

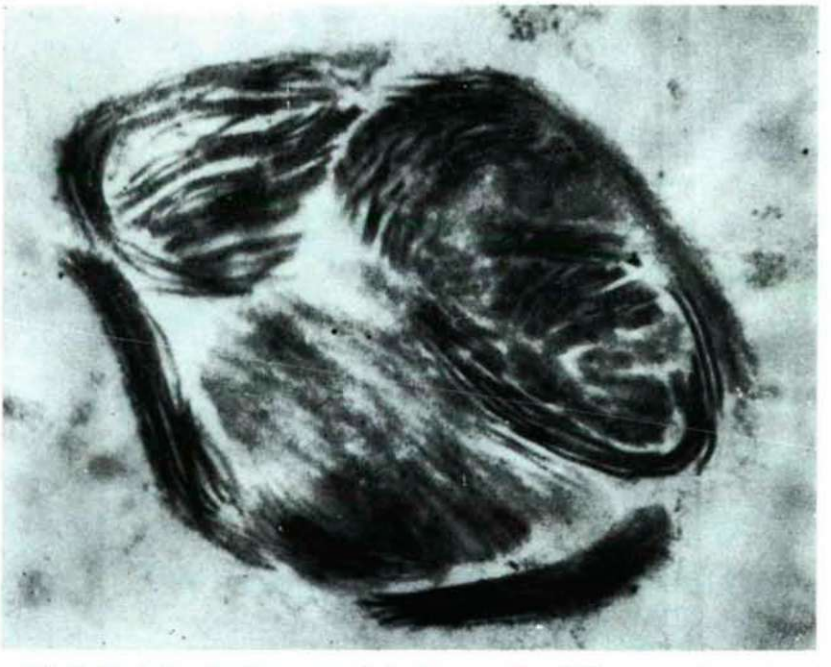
Plate II

Transforming crystalline bodies. x28 000.

Plate III



1

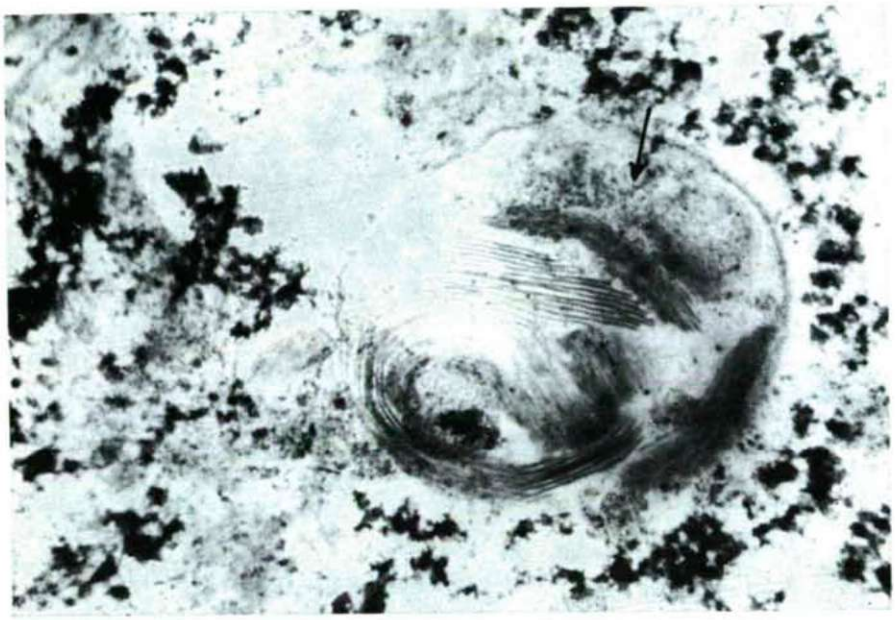


2

Fig. 1. Crystalline bodies progressively disintegrating. (ER — endoplasmatic reticulum, N-nucleus). x16 000.
Fig. 2. Bodies of a loose membrane — system. x64 000.

Plate IV

1

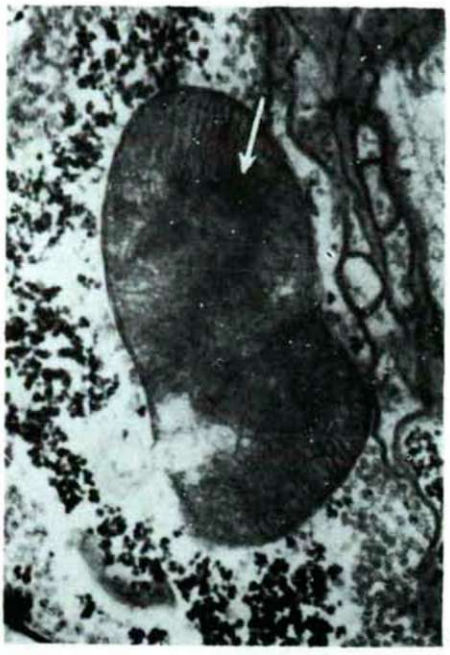


2

Fig. 1. In the centre of crystalline bodies dense granules appear at first. (Granules are indicated by arrows). x36 000.
Fig. 2. A gradually evacuating body. (The arrow is pointing at the matrix of changing density.) x36 000.

Plate V

1



2

3

Fig. 1. A transforming mitochondrium from the thoracic ganglion-cell of the larva. x20 000.
Fig. 2. A transforming mitochondrium. (The arrow is pointing at the change in density of membranes.) x28 000.
Fig. 3. A transitory form between the mitochondrium and the paracrystalline body. x48 000.

are in fact, transforming, changing mitochondria, with insertion of the paracrystalline bodily state.

The literature data indicate that the cytosomes appear as a "Stoffwechseldepot", mostly under anoxic conditions (NOLTE et al., 1965; ZS.-NAGY, 1975). The anoxic conditions are explained by the low development of the metabolic organelles of the individuals examined.

Whether these organelles conform in full with the cytosomes described from molluscs (Mollusca) we want to decide later, by means of histochemical and experimental investigations.

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DATA ON THE ECOLOGICAL ENERGETICS OF FORMICA PRATENSIS RETZ. (HYMENOPTERA: FORMICIDAE) IN THE PSAMMOPHILE ECOSYSTEMS OF THE SOUTHERN HUNGARIAN PLAIN

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Abstract

The polygynous and polycalic colonies of *Formica pratensis* RETZ. occur in grassland ecosystems, but the workers collect a large part of their food in the nearby planted woods of *Pinus silvestris*. In this way, they establish a contact of material flow between the two different ecosystem types. A maximum can be observed at the end of May and early June in the annual course of their feeding activity, and at 9 and 14 o'clock in daily rhythm. On a single occasion the foragers consume food amounting on average to 19.3 per cent of their body weight, that is 0.485 mg (1.902 cal) in dry weight. The annual consumption of a colony of a hundred thousand individuals ($1.13 \cdot 10^5 - 2.04 \cdot 10^5$), consisting of 12 nests, selected for investigations into their food consumption, is between 13,08 and 22.63 kg. This means as referred to the feeding area, an amount of 2.54—4.39 g/sq m (9967 to 17 524 cal/sq m). *F. pratensis* mostly take part (48.4 per cent) as secondary and tertiary consumers in the grazing food chain, but their honeydew consumption is also very considerable (39.2 per cent). The elimination of the population is mostly caused by the woodpeckers *Picus viridis* L. and *Dendrocopus major* L., by the activity of wich the populations of nests can be reduced by about a half. Owing to the woodpecker-induced elimination, a minimum 1.6 per cent ecological effeciency (100 P/C) is necessary to ensure the survival of colonies in an unchanged size.

Introduction

The particularly important role of ants in the material and energy flow in some ecosystems is proved by the results of research obtained so far in the course of structural and functional studies on terrestrial ecological systems. With his general model GÖSSWALD (1965) outlinex the activity of *Formica* s. str. species in the forest-ecosystems. In respect of *pratensis*, food consumption investigations were carried out by EIDMANN and STAEGER (STITZ, 1939). AYRE (1966) investigated the connection between the colony size and food consumption in three ant species, under artificial conditions. PETAL (1967, 1972) calls attention not only to the co-sumption and productivity parameters of *Myrmica laevinodis* NYL. population, but also to the role of ants in regulating the secondary production of grassland ecosystems, in her papers written with co-workers (PETAL at al., 1971; KAJAK et al., 1971, 1972). DLUSSKY and KUPIANSKAYA (1972) pointed out the importance of protein food for *Myrmica* species. BRIAN et al. (BRIAN, 1967, 1972; BRIAN et al., 1967, 1974) have investigated the size, productivity and population turnover of populations of *Tetramorium ceaspitum* LATR. and *Myrmica* species in the lowland plains of Southern England. NIELSEN (1972a, b, 1974a, b, 1975) has examined the

productivity and energy flow of *Lasius alienus* populations in the psammophile ecosystems of Denmark. The energetics of *Pogonomyrex badius* were elaborated by GOLLEY and GENTRY (1964) in old fields.

In respect of the *Formica pratensis* species, laboratory investigations into ecological energetics were performed by HORN (1972). GALLÉ (1973, 1976a) described the thermoregulation and rhythm of the feeding activity in the nests of this species.

Formica pratensis is the only considerable species of the grassland and forest ecosystems in the Hungarian plain, belonging to the *Formica* s. str. subgenus. The aim of the present investigations was to determine the food consumption and other ecological energetics parameters of this ant species under natural conditions.

Materials and Methods

The investigations were performed between 1971 and 1975, into ant colonies in the *Astragalo-Festucetum sulcatae* and *Festucetum vaginatae stipetosum* ecosystems.

The colonies were of polycalic and polygynous character. A large part of the food was collected by the workers in the nearly planted *Pinus silvestris* grove. Thus apart from the role of pratensis establishing a contact of the material flow for both types of ecosystems between the natural grassland and the planted wood, their ecological role in the lowland pine plantations can also be concluded from the results of the investigations.

The food consumption was measured in full in a polycalic colony, consisting of eight major and four smaller permanent nests and a number of provisional branch nests. In other colonies only "point investigations" have been performed with the intention of comparing these.

In the course of measuring the food consumption, we considered assessment of the following parameters as most important:

1. The rhythm of feeding activity of the colony.
2. The amount of material removed (MR) and really consumed (C) by individuals.
3. The qualitative composition of the food.

The seasonal and daily rhythms of feeding activity were established on the basis of numerical fluctuations of the individuals leaving and returnung the colony on the food-ways (GALLÉ, 1976).

The quantity of material removed (MR) and the consumption (C) were estimated on the basis of difference of the individuals leaving the colony hungry and those returning with full crops, in each case with a minimum of thirty individuals. Taking into consideration that the difference in weight between the hungry individuals and those returning with food can also be a result of a constitutional difference, in order to avoid any mistake, we corrected the weight-data by means of the head-width index, which is proportionate to the size of the individuals. According to this, the consumption value is to be determined in the following way:

$$C = g_c - \frac{1}{h_o} \cdot g_o \cdot h_c$$

where C=consumption; g_c=dry weight of the individual returning with food; g_o=the average starving weight, its value being 2.4089 mg; h_c=the average head-width, *i.e.* the head-width of the individuals representing the average starving weight. To the 2.4089 mg average individual weight a head-width of 1.65 mm belongs. With this method, having duly exact g_o and h_o data, we could establish even the food amount consumed by a single ant. The weight of the material quantity removed (MR) was calculated from the weight of the food remainder carried into the nest in the mandibles but not being consumed, too.

The qualitative composition of the food was also determined from the food remainder carried into the nest in the mandibles. However, ants carry the largest part of their food not in the mandibles but in the crop, the "social stomach". It is supposed by some authors that the food carried in the mandibles is the insect food and the excretion of Aphids is carried into the nest in their crop. With regard to the fact that the amount of material carried in the crop is the vast majority of the MR, it seemed to be necessary to analyse the contents of the crop as well, in order to decide whether they contained sugar or some food of other character. The analysis of the crop contant was carried out

with a simple sugar-test by means of guttadiaphot (SZALAI—FRENYÓ, 1962); hence it could be decided what percentage of the individuals returning into the nest had consumed honeydew.

The number of individuals in the nests necessary for determing B_0 was estimated with Lincoln's index, and the number of feeding individuals was determined with a method based essentially upon Horstmann's investigations (1974), assuming that the active feeders leave the nest, in the case of two activity maxima daily, twice a day. With regard to the very high individual number in the colony both estimations have an informative character rather but in relation to the order of magnitude.

To determine the elimination (E), the nests were covered with guard-nets, to keep the woodpeckers off (1972—1973), and after removing the nets we assessed the decrease in the number of colony by means of the decline in the number of feeding individuals.

The material quantities figuring below are everywhere given in dry weight. The calorific contents of biomass amounts, as well as those of the other substances occuring, were determined with Phillipson's Gentry-made microbomb calorimeter with combustion in oxygen in the bomb under 35 atm.

The denomination and interpretation of the parameters in the material and energy flow of the population are applied according to PETRUSEWICZ (1967a, b), as well as PETRUSEWICZ and MACFADYEN (1970).

Results

The results of the feeding activity were reported in an article published previously (GALLÉ, 1976a). According to this, the feeding activity changes seasonally and in a daily course, as well. In an annual relation, a peak develope in late May or early June, in the daily course, two maxima can be observed, at about 8—9 a.m. and 2—3 p.m.

The dry weight of the food consumed by the individuals is on average $19.3 \pm \pm 3.66$ per cent of the weight of the feeding workers. This is 0.485 ± 0.087 mg, or 1.902 cal individually. The food amount consumed by the full colony changes in parallel with the rhythm of the feeding activity. In accordance with the higher number in the colony ($2.04 \cdot 10^5$ individuals), in the years when a stronger protection was ensured by the net, the material amount consumed was also larger; it varied between 68 and 419 g/day during the year, while after removal of the nets a colony of $1.13 \cdot 10^5$ consumed between 13.85 and 131.90 g/day (Fig. 1).

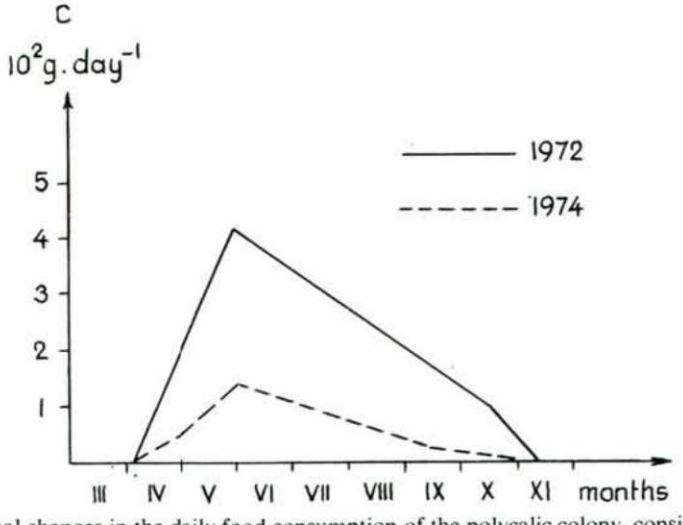

Fig. 1. Seasonal changes in the daily food consumption of the polycalic colony, consisting of twelve permanent nests of *Formica pratensis*, in natural (1974) and net-covered states (1972).

The cological role of *Formica pratensis* can be established on the basis of the qualitative composition of the food. The vegetable parts amount 4.98 per cent of the materials carries into the colony (Table 1). This is, therefore, the primary consumer activity of pratensis. As, however, it does not consume the decisive majority of these substances, but probably uses them for building nests, this amount is NU from the point of view of the population. This species is active as secondary consumer of the grazing food chain in 36.11 per cent of the total MR. From among the pytophages consumed, the *Lepidoptera* larvae amount to 35.09 per cent. In addition predation of *Aphidina* is also very considerable (23.24 per cent). From among the beetles, representing a very high ratio (14.91 per cent of the total phytophages, Table 2), *Peritelus familiaris* amounts to 6.14 per cent, i.e. approximately half of all beetles consumed. The tertiary consumer activity is 12.40 per cent of the total activity (Table 1); from the secondary consumers pratensis cosume other *Formicidae* in largest quantity (Table 3); these mean 64.61 per cent of the food cosisiting of secondary consumers, 7.403 per cent of the total food. The *Formicidae* consumed are: *Leptothorax unifasciata* LATR., *Lasius alienus* FÖRST., *Lasius emarginatus* OL., *Lasius brunneus* LATR., *Formica cunicularia* LATR., and *Formica fusca* L.

The participation in consuming detritus means 7,3 per cent of the food of

Table 1. Percentage distribution of the ecological activity of *Formica pratensis*

activity	per cent
primary consumer	4.979
secondary consumer	36.112
tertiary consumer	12.398
decomposer	7.330
honeydew	39.180
total	99.999

Table 2. Percentage composition of the foodstuffs consumed in the course of secondary consumer activity of Formica pratensis. The foodstuffs specified according to insect orders originate from 42 primary consumer niches. n = 228

type of food	per cent
Orthoptera	3.508
phytophagous Heteroptera	3.508
Aphidina	23.245
other Homoptera	1.315
Coleoptera adults	14.912
Coleoptera larvae	0.877
Lepidoptera adults	0.877
Lepidoptera larvae	35.087
Lepidoptera pupae	0.438
Diptera	9.649
Hymenoptera	3.508
Others	3.070
total	99.994

Table 3. Activity of the tertiary consumer *F. pratensis*. The foodstuffs specified originate from 24 different secondary consumer niches. n=65

type of food	per cent
carnivorous Heteroptera	1.538
Neuroptera	6.153
Coleoptera	6.153
Diptera	3.076
Formicoidea	64.615
other Hymenoptera	6.153
Araneidea	12.307
total	99.995

Table 4. The decomposing activity of *F. pratensis*. n=21

type of food	per cent
Isopoda	14.285
Diplopoda	23.809
Blattidea	14.285
Coleoptera	19.047
Acari	14.285
material regurgitated by birds	14.285
total	99.996

Formica pratensis. Within this, it removes the corpses of insects and other animals, primarily by consuming the *Diplopoda, Isopoda,* and *Coleoptera* corpses (Table 4). The consumption of the animal of other origin (bird-regurgitation) is comparatively subordinate: 14.29 per cent of the decomposing activity and 0.53 per cent of the total food. The cosumption of honeydew is also to be included in the decomposing activity, amounting, according to the sugar test, to 39.1 per cent of the total food (Table 1).

The total biomass of the colony in 1972—1973 was on average 493.54 g (2615.7 kcal), represented by 204 thousand. This number was reduced in 1974, after removal of the guard-nets, to 113 thousand, with 273.84 g (1451.3 kcal). On the basis of this, it can be established that value B was diminished by woodpeckers by approximately 50 per cent. In order, therefore, that the colony should remain unchanged or even increase, the ratio P/C must at any event be higher than 1,67 per cent, so much the more so because, apart from birds, there are other elimination inducing factors, as well. The ecological effeciency of about 2 per cent (ratio 100 P/C) is characteristic of ants according to other ant-energetics works too (PETAL, 1974, TIMÁR, 1974, GALLÉ, 1976). From among the two woodpecker species already mentioned, the more considerable predator of *Formica pratensis* is *Picus viridis*. As regards other birds, *Parus major* L. and *Passer montanus* L. also feed in the nests

of pratensis occasionally. According to de BRUYN et al. (1972), the green woodpecker consumes a maximum of 22—36 · 10^3 ants from the nest of *Formica rufa* L. in one winter; the average consumption however, is lower than this. According to the present investigations, 91,000 individuals perished as a result of the activity of woodpeckers. Taking into consideration the twelve nests, this is 7.58 · 10^3 ants a nest. In order of magnitude, this agrees therefore with the data of de BRUYN et al. As compared with the nest population of pratensis, however, many more individuals perished (44 per cent of the population of the colony) than it was observed by de BRUYN et al in the case of rufa, where this ratio was about 5 per cent. In this high ratio in the case of pratensis, another factors besides the food consumption of woodpeckers may have been that in winter the nests are ventilated by woodpeckers which bore holes in the nests, in this way putting an end to their thermostatic control. Many workers perish as a result of this.

The material and energy flow of the *Formica pratensis* investigated may therefore be summarized as follows (Fig. 2): The annual consumption of the twelve

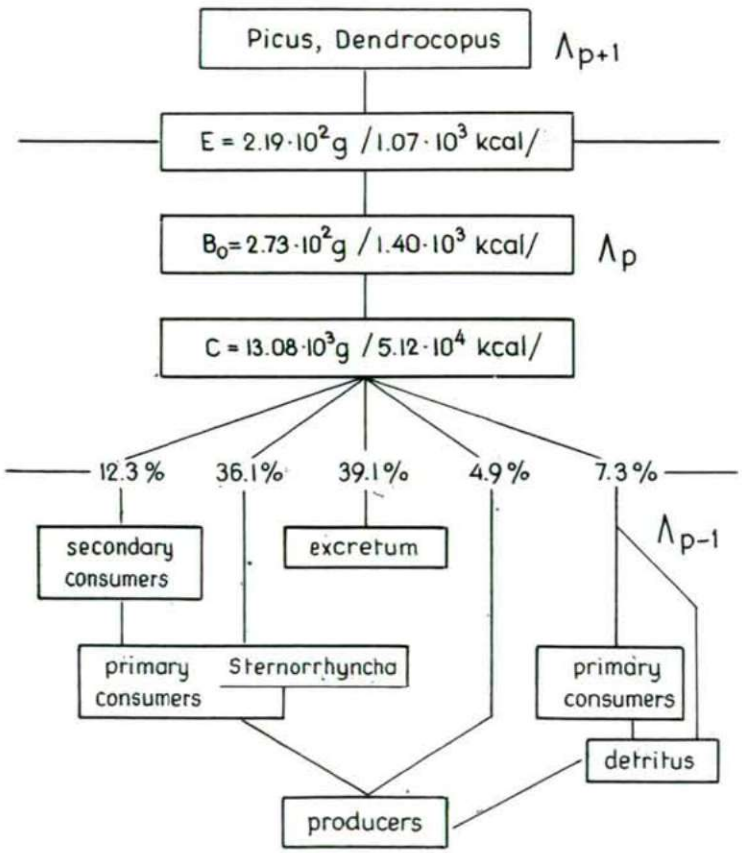

Fig. 2. Outline of the material and energy flow of the polycalic colony of *Formica pratensis*. *A*p = energy level of *F. pratensis*.

nests creating the colony was 13.08 kg. This amount, if the individual number within nests is increased by applying guard-nets, as in the years 1972 and 1973, may increase to even 22.63 kg. It is shown by this that if we wish to increase the effeciency of the activity of *Formica pratensis,* for instance in order to give biological protection to pine-plantations, by using nets to eliminate woodpeckers, the volume of the consumption can be raised to almost the double. The above consumption data mean in a square metre quantities of 2.54 g (9967 cal) and 4.39 g (17 524 cal), respectively. The standing crop of the colony (B_0) was $2.73 \cdot 10^2$ g ($1.4 \cdot 10^3$ kcal); this, in a protected state, may rich $4.93 \cdot 10^2$ g ($2.6 \cdot 10^3$ cal). The extent of the bird-induced elimination (E) appeared to be $2.19 \cdot 10^2$ g ($1.07 \cdot 10^3$ kcal).

Conclusions

In the course of the investigation into the material and energy flow of the colony of *Formica pratensis,* the parameters B_0, C and E were determined.

1. *Formica pratensis,* in its ecological activity, is decisive by a secondary consumer. It plays a particular considerable role in regulating the secondary productivity of pine-plantations.

2. A considerable part of the food is honeydew (39.2 per cent).

3. The annual food consumption of the polycalic colony is of the order of 10^4 kcal.

4. Elimination is mainly induced by woodpeckers. Its value is of the order of 10^3 kcal a year.

5. The production necessary to preserve the colony is larger than $0.016 \cdot C$ a year.

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DISPERSION OF THE NESTS OF AN ANT SPECIES (HYMENOPTERA: FORMICIDAE)

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Abstract

On the basis of dispersion-index, Morisita's index and the "mean crowding", the dispersion of nests of the very high density population of *Lasius alienus* FÖRST. (1.27 nests/sq. m) in the *Festucetum vaginatae* plant association turned out to be of uniform type. However by the fitting-test to positive bionomial distribution and to that of Poisson, random dispersion was rendered more probable. In this way the results of dispersion index and the fitting-test to some extent contradict each other. It is also true for the *L. alienus* population that an increase in density involves a change in the uniform direction of dispersion.

Introduction, Methods

Some publications are known concerning the dispersion of ants. BRIAN (1956) studied the distribution of *Myrmica rubra, M. scabrinodis,* and *Leptothorax acervorum,* by investigating the fitting to Poisson's distribution. BARONI—URBANI (1969) identified the dispersion of *Lasius alienus* and *Tetramorium ceaspitum* with the $\varkappa^2$-test and Morisita's index; PETAL (1972) applied the dispersion index $s^2/\bar{x}$ to study the dispersion of the nests of *Myrmica laevinodis*; GALLÉ (1975) investigated the connection between the density and the dispersion-index in five ant species. As the type of dispersion in a homogeneous or neraly homogeneous environment may be an index of the intraspecific competition (BRIAN, 1965; GALLÉ, 1975), a knowledge of the dispersion is essential in the ecological study of ants.

In the present work, the dispersion of nests of the ant species *Lasius alienus* FÖRST. in the phyto-association *Festucetum vaginatae* is demonstrated. As pointed out by NIELSEN in his papers on the density, biomass and productivity of *Lasius alienus* populations in the grassland ecosystems in Denmark (NIELSEN, 1972a, b, 1974a, b), in habitats of sandy soil the nests of this ant cannot be delimited sharply from one another. As there are some groups with larger or smaller individual members in the soil, it is difficult to define the limits of nests. In the course of the investigation, therefore, only those groups of individuals were qualified as nests where broods could be found.

Since the nest-density of the *Lasius alienus* population is very high in the course of recordings the sampling size selected as "minimiareal" was 4 sq. m (a square of 2×2 m). Thirty six samples like this were made.

Several methods are known for identifying the three kinds of dispersion archetypes: the random, clumping and uniform ones. From among these in evaluation

of the data the following were applied: dispersion index and $\varkappa^2$-test (SOUTHWOOD, 1968), Morisita's index (ibid.), "mean crowding" (LLOYD, 1967) and fitting-tests to Poisson's and positive binomial distributions (DOBÓ-ZAJTA, 1958; ANDREWARTHA, 1961; MACARTHUR and CONNELL, 1967; GALLÉ, 1973).

Results and Discussion

In the course of recording, the following characteristic features were found:

total nest number (Σx)	183 nests
sample average ($\bar{x}$)	5,083 nests/4 sq. m
sq. m average ($\bar{x}$/sq.m)	1,270 nests/sq. m
standard deviation (s)	1,158
variance (s^2)	2,493

On the basis of the above traits, according to the formula

$$N = \left(\frac{t.s}{D.\bar{x}}\right)^2$$

(SOUTHWOOD, 1968), where D=0,1, 39 samples are necessary at a 5 per cent significance-level (t=2,03), and 27 samples at a 10 per cent significance level (t=1,69). Thus, the 36 samples recorded at a 5 per cent significance level may be considered satisfactory.

The data of the dispersion index

$$V = \frac{s^2}{\bar{x}}$$

are contained in Table I. It is also to be seen from the Table that the value of V is much below 1, while the value of $\varkappa^2$ falls outside the 0.05 and 0.95 limits of the table. Therefore, by reason of the test, the probality of Poisson's distribution can be rejected with 95 per cent certainty and the low value of V indicates a uniform dispersion.

The form of Morisita's index is as follows:

$$I_\delta = N\frac{\Sigma x^2 - \Sigma x}{(\Sigma x)^2 - \Sigma x} \tag{1}$$

The test of the significant different from the random one is:

$$F_0 = \frac{I(\Sigma x - 1) + N - \Sigma x}{N - 1} \tag{2}$$

The value of I_δ, on the basis of (1), is 0.987. The result of the F test, according to (2), is 0.922, i.e. non-significant. However as pointed out by BARONI—URBANI, equation (2) is not suitable for testing the significante of uniform dispersion.

Lloyd's charactersistic, "mean crowding", (1967) is very suitable for discribing dispersion and particulary the ratio $\overset{*}{m}/m$, named by "patchiness". In this case, the

Table 1. Results of the dispersion index (V) and $\varkappa^2$-test $\varkappa^2_p$ = values of the $\varkappa^2$-table; $\varkappa^2_{exp}$ = calculated from the dispersion index; df_1 = degrees of freedom from the table; df_2 = real degrees of freedom

data	value	df_1	df_2
$\chi^2_p(0.95)$	18.5	30	35
$\chi^2_p(0.05)$	43.8	30	35
χ^2_{exp}	17.2	30	35
V	0,49	—	—

real "mean crowding" is not taken into consideration, but an estimated value of this:

$$\overset{*}{x} = \frac{\Sigma x_i^2}{\Sigma x_i} - 1$$

For the dispersion of *Lasius alienus* nests this is 4,489 and $\overset{*}{x}/\bar{x}$ is 0,8832 i.e. smaller han unity. This similarly points to a uniform dispersion.

Table 2. Fitting of the observed data to the probability distributions. x/sample = nest number/sample; 0_i = frequency observed; $E_{i\ Poisson}$ = frequency calculated on the basis of Poisson's distribution; $E_{i\ pos.b.1.}$ = frequency calculated on the basis of positive binomial distribution; $E_{i\ pos.b.2.}$ = frequency calculated on the basis of positive bionomial distribution in the domain between 0 and 7 nests/sample

x/sample	0_i	$E_{i\ Poisson}$	$E_{i\ pos.b.1.}$	$E_{i\ pos.b.2.}$
0	0	0.219	0.057	0.006
1	1	1.119	0.452	0.118
2	3	2.854	1.661	0.825
3	4	4.852	3.689	3.200
4	7	6.188	5.532	7.480
5	11	6.307	5.902	10.480
6	5	5.364	4.591	8.150
7	2	3.909	2.623	1.060
8	0	2.491	1.092	—
9	2	1.415	0.325	—
10	0	0.720	0.065	—
11	0	0.348	0.078	—
12	1	0.140	0.000	—

Both on the basis of above facts, and as a result of the negative k-value of the negative binomial distribution used for identifying the clumping dispersion, the probality of a clumping dispersion can significantly be rejected. Thus, from among the theoretical probality distributions, Poisson's and positive binomial fitting are to be performed. The data of the fitting test are contained in Table 2. According to the fitting investigation performed with the x^2 test, for Poisson's distribution $\varkappa^2 = 11.03$; $0.05 < p < 0.10$. Accordingly, although positive binomial

distribution cannot be rejected significantly, Poisson's distribution and hence random dispersion seem to be more probable. The results of this test are therefore at variance with the $\varkappa^2$ test of the dispersion index, where a significant deviation from random dispersion was observed. On graphical fitting, however, if the 8 and 12 nests/sample extreme values obtained in the course of recording are not taken into consideration, positive binomial distribution seems to give a comparatively good approximation. However the probality obtained by the $\varkappa^2$ fitting test is a low one, even in this way (Fig. 1:4). The graphical fitting to Poisson's distribution — with the exception of the observed points (5.11) — is similarly closed (Fig. 1:2). According to the available literature data, clumping dispersion of ant nests was investigated only by PETAL (1972), in the case of *Myrmica laevinodis*. The density of the population studied by her, however, was very low. On the other hand, BRIAN (1956), in the case of *Myrmica* species, too, observed uniform and random dis-

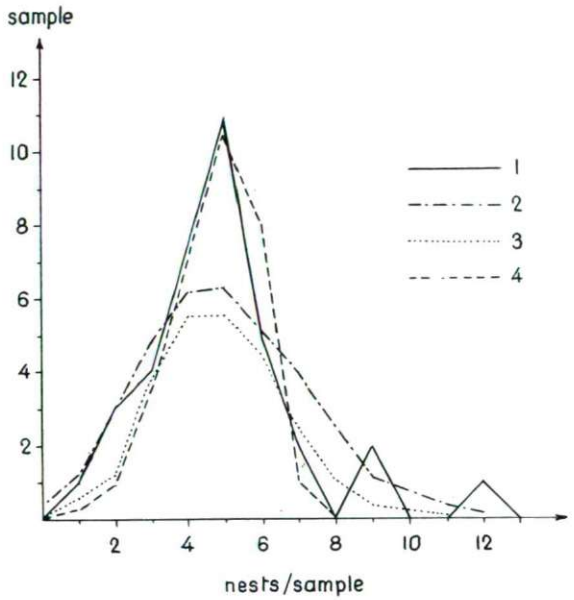

Fig. 1. Graphical fitting. 1 = data observed, 2 = poisson's distribution, 3 = positive binomial distribution, 4 = positive binomial distribution in the domain between 0 and 7 nests/sample ($E_{i\ pos.b.2.}$ values).

persion. BARONI—URBANI (1969) investigated *Lasius alienus* populations with a density of about 0.3 nest/sq.m. in *Brachipodietum* and *Festucetum* phyto-associations. On the basis of the $\varkappa^2$-test of the V index, the dispersion proved to be a random type.

According to the results obtained with the same method, the dispersion of the *L. alienus* population investigated in the present paper is uniform, and its density is much higher (1.27 nests/sq. m). Comparing the data of PETAL and BRIAN concerning the *Myrmica* species, as well as the values of present paper, with Baroni—Urbani's *L. alienus* data, it is seen that in the case of a higher density the dispersion

is shifted to be uniform — to wich attention was called with the inverse proportionalty of the density and dispersion index (V) in a previous paper (GALLÉ, 1975). This connection between the density and dispersion index can be explained via the density-dependent character of the intraspecific competition inducing a uniform dispersion.

Conclusions

In respect of the dispersion of *Lasius alienus* population of very high density, the following conclusions may be drawn:

1. On the basis of Morisita's index, mean crowding analysis and the dispersion index, the dispersion proved to be uniform.

2. The fitting study into the theoretical distributions, on the other hand, makes Poisson's distribution more probable than the positive binomial one. Negative binomial dispersion can be rejected because of the results of every test and the negative value of "k".

3. On the basis of the dispersion index, comparing the present investigations with Baroni—Urbani's results (1969), an inverse proportionality may be observed between the density and dispersion index.

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RESPIRATION AS ONE OF THE MANIFESTATIONS OF THE GROUP EFFECT IN ANTS

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Abstract

The oxygen consumption of workers of *Camponotus vagus* LATR., *Formica pratensis* RETZ., *Formica cunicularia* LATR. and *Formica fusca* L., measured with Wartburg's technique in the interval 15—35 °C, varies with the temperature according to a logistic curve. The O_2 consumption measured in $\mu l \cdot mg^{-1} \cdot h^{-1}$ is inversely proportional to the number of worker ants put in one respiration chamber. This connection may be described by a hyperbolic curve. If the individual number increases, the hyperbola approaches a particular "group respiration" value.

Introduction

Study of the ecological energetics and production biology of ants necessitates the determination of the quantity of energy (R) released in the course of respiration. Many papers published on this subject therefore deal with respiration from an energetical approach. GOLLEY and GENTRY (1964) measured the oxygen consumption in a bioenergetical investigation of *Pogonomyrmex badius*. MALDAGUE et al. (1967) studied the respirations of five Canadian ant species as a function of temperature. As regards the European species, first the respiration of *Formica polyctena* was measured by SCHMIDT (1967), then that of *Lasius alienus* by NIELSEN (1972). JENSEN and NIELSEN (1975) examined the oxygen consumption in eight ant species as a function not only of temperature, but also of body-size.

The aim of the present investigations was to investigate the temperature-dependence of the respiration, and also to measure the difference between the oxygen consumptions of solitary ant workers and those staying in a group, on *Camponotus vagus* LATR., *Formica pratensis* RETZ., *F. cunicularia* LATR., and *Formica fusca* L.

Warburg'a technique was applied at temperatures between 15 and 35 °C. On each occasion, ten parallel measurements were performed and four further vessels were used as thermobarometers. Depending upon the species and individual number, the individuals put in the respirometer were made accustomed to the respirometer for 1 to 14 hours before measurement, so that the results should not be influenced by the excitement of being put into the equipment. A total of 504 measurements were made.

Results and Discussion

JENSEN and NIELSEN (1975) found a correlation of the form

$$\log y_w = 0.0491\,t - 0.9111$$

between the temperature and the oxygen consumption in the interval between 5 and 25 °C. The present investigations show that in the range between 15 and

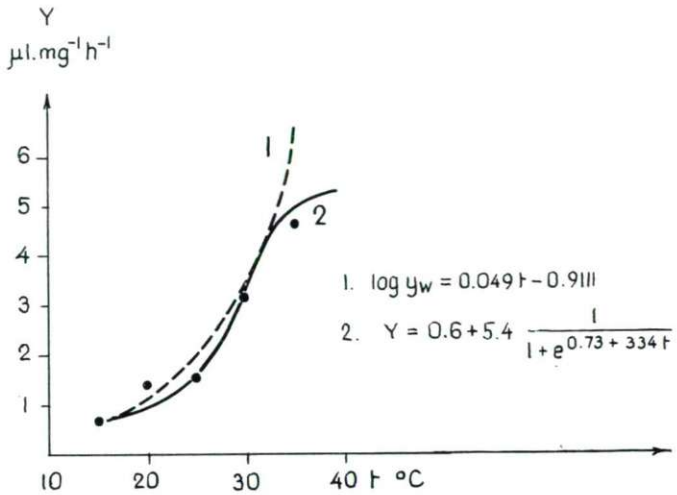

Fig. 1. Comparison of Jensen and Nielsen's (1975) equation (1) with the values obtained for *Formica fusca* (2).

35 °C the correlation can be better approximated to by a logistical function (Fig. 1). The functions obtained for the individual species were as follows:

Formica cunicularia:

$$Y = 0.45 + 3 \frac{1}{1+e^{16.3-0.6523t}}$$

Formica pratensis:

$$Y = 1.70 + 3.1 \frac{1}{1+e^{13.74-0.547t}}$$

Formica fusca:

$$Y = 0.60 + 5.4 \frac{1}{1+e^{0.73-0.334t}}$$

Camponotus vagus:

$$Y = 1.00 + 4.1 \frac{1}{1+e^{7.694-0.345t}}$$

where Y = the oxygen consumption in $\mu l \cdot mg^{-1} \cdot h^{-1}$, calculated on the dry weight; $e=2.718$, the base of natural logarithms; t=temperature in °C; the significance of fitting of the data measured to the function for *F. cunicularia* is $p<0.1$; for *F. pratensis* $p<0.05$; for *F. fusca* $p<0,01$, and for *C. vagus* $p<0.001$. A sigmoid curve was obtained by CSOKNYA (1973) and CSOKNYA and HALASY (1975) for the connection between temperature and respiration for *Palingenia,* as well.

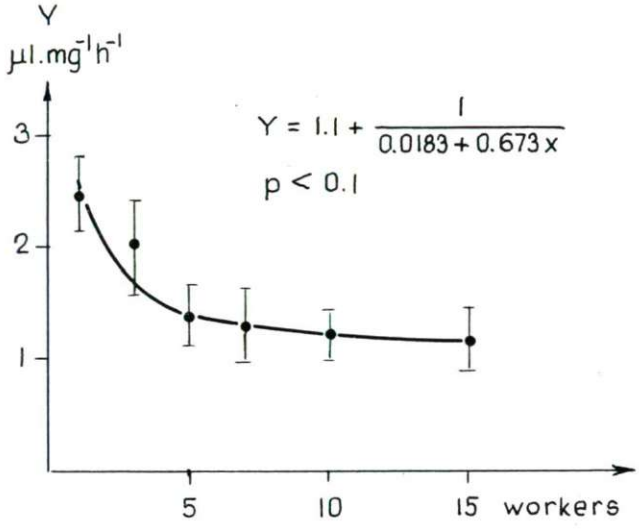

Fig. 2. The function obtained for the correlation between the individual number of *F. cunicularia* and the O_2 consumption.

In the investigation into the connection between the individual number in a respirator chamber and the oxygen consumption, 1, 2, 3, 5 or 10 ant workers were placed into a chamber at 25 °C and the respiration was measured. In addition 7 and 15 individuals were also applied in the case of *F. cunicularia*; with *C. vagus,* on the other hand, for technical reasons the maximum number of individuals was five. An inverse proportionality was found for the connection of the individual number and the respiration, approximated to by a hyperbolic function. Figure 2 shows the data obtained for *F. cunicularia.* The hyperbolic approximation is non-significant ($p>0.1$) only in the case of *F. pratensis,* and thus, instead of the equation:

$$Y = 0.71 + \frac{1}{0.526 + 0.246\,x}$$

the straight line $Y=2.215-0.149x$ means a mathematically better approximation ($p<0.05$); however this would mean that for a certain individual number there would be no oxygen consumption, and therefore, from biological considerations, even in this case the hyperbolic approximation is considered more suitable.

WILSON (1971), refining GRASSÉ's definition, suggested the following definition of a group effect: "a group effect is an alteration in behavior or physiology within

a species brought about by signals that are directed in neither space nor time". In this sense the effect of the individual number on the respiration, as a non-directed physiological alteration appearing in a group, must be classified as a group effect.

In the respiration, as a manifestation of the group effect, two values in particular are held to be important:

1. The individual number at wich the slope of the hyperbolic curve suddenly decreases. This "critical individual number" was generally five for the species investigated, but 6—7 for *F. pratensis*.

2. The oxygen-consumption value approximated to by a hyperbola is the value of the "group respiration" characteristic of the species. This was 0.7 *(F. fusca)*, 1.0 *(F. pratensis)*, 0.8 *(C. vagus)* and 1.1 *(F. cunicularia)* $\mu l \cdot mg^{-1} \cdot h^{-1}$.

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NEW SPECIES AND SOME REMARKS ON THE GENUS CEROPALES LATREILLE (HYMENOPTERA: CEROPALIDAE)

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Abstract

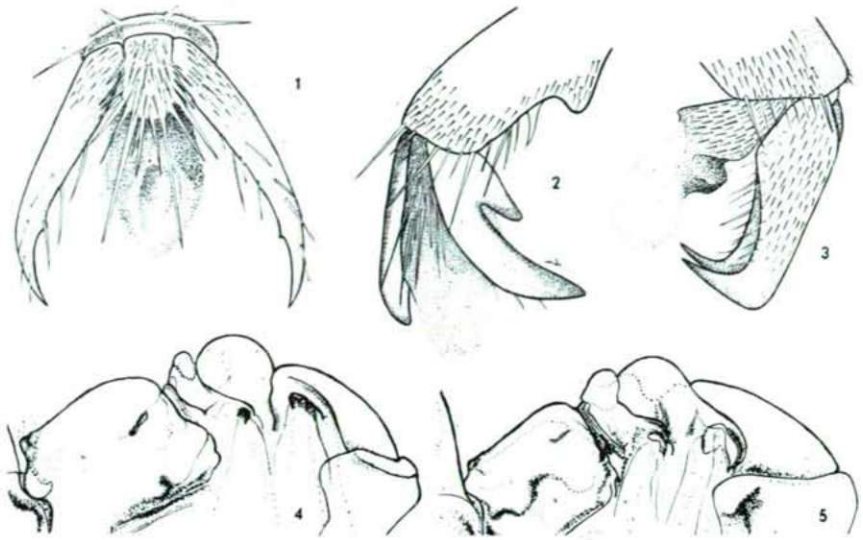
Author discusses the species belonging to the genus *Ceropales* LATREILLE. He considers all the subgenera of Wolf's and Priesner's schemes as independent, higher taxa, i.e. genera. Distribution data appended and designations of holo- and lectotypes are given for the following species: *C. turcomanus, C. magnificus, C. altaicus, C. r. ruficornis, C. r. gilvus, C. sibiricus, C. erythropodus.* New taxa are *C. trjapitzini* sp. n., *C. maculatus turcmenensis* subsp. n., *C. albicinctus wolfi* subsp. n., *C. a. mediterranicus* subsp. n. Author describes the male of *C. bicoloripes* MÓCZÁR, establishes several new statuses and complete them with distributions data.

The old genus *Ceropales* LATREILLE, 1796 is widespread all the world and the more than 100 at present known species are morphologically so different that — similar to the earlier homogeneous genera *Odynerus, Crabro* etc. — it is reasonable to divide it into independent genera (MÓCZÁR 1978). The principles of the distribution are given by the subgenus scheme of WOLF (1965) and PRIESNER (1969). Only those species of *Ceropales* s. str. are discussed here, which are noteworthy either from systematical, or from zoogeographical point of view, and are found in the following collections (after the locality names in brackets): the Zoological Institute of the Academy of Science, Leningrad (V. TOBIAS), Rijksmuseum von Natuurlijke Historie, Leiden (I. T. WIEBES), Eidg. Technische Hochschule, Zürich (P. BOVEY and W. SAUTER), Naturhistorisches Museum Zoologische Abteilung, Wien (M. FISCHER), Zoological Department of the Hungarian Natural History Museum, Budapest (J. PAPP). I express my grateful acknowledgements for the loan of the material. The South African and American species will be treated later on. The following characters are considered as the most important ones of the *Ceropales* genus.

Ceropales LATREILLE

Ceropales LATREILLE, 1796, Préc. car. gén. Insect.: 123 nr. XXV.
Ceropales subgenus *Ceropales:* 1965, WOLF, Nachr. Nat.-Mus. Aschaffenburg, H. *72:* 37
Ceropales s. str.: 1969, FRIESNER, Naturkundl. Jb. Linz, 115, 118 ♀♂

Both claws of fore (♀) and middle (♀♂) tarsus as well as outer claw of fore tarsus (♂) with a short erect and acute subapical tooth (Fig. 1); inner claw of fore tarsus (♂) very deeply split owing to the unusually large, not truncate inner tooth basally (Fig. 2). Sometimes (in ♂ of the *fulvipes* group) both claws of middle tarsus specialized and similar to the very deeply split tooth of the fore inner claw of the male belonging to another species. Inner side of last tarsal joint of fore leg



Figs. 1—3. Claws of *Ceropales* LATREILLE, 1 = middle leg (♀♂); 2 = inner claw and last tarsal joint of fore tarsus (♂); 3 = hind leg. — Figs. 4—5. Upper margin of propodeum-mesonotum 4 = *Ceropales maculatus maculatus* FABRICIUS; 5 = *C. ruficornis ruficornis* GUSSAKOVSKIJ (Figs. 1—3: MÓCZÁR, 1967, Figs. 4—5: A. FAZEKAS).

deeply emarginated (Fig. 2). Both claws of the hind tarsus rectangularly curved (Fig. 3). Labrum large, conspicuously exposed; eyes divergent dorsally, inner margins concave above. Propodeum gradually convex in lateral view (Fig. 4) or when distally more flat than remarkably convex basally (Fig. 5), i.e. arched and joining postnotum nearly rectangulary. Last abdominal segments (♀) strongly compressed.
Typ. gen.: *Ceropales maculatus maculatus* (FABRICIUS), 1775 ♀♂.

Ceropales variegatus (FABRICIUS)

Evania variegata FABRICIUS, 1798, Suppl. ent. syst.: 241 nr. 2—3
Ceropales variegatus: 1954, MÓCZÁR: Folia Ent. Hung., (S.n.) *7*: 149
Ceropales (Ceropales) variegatus: 1965, WOLF, Nachr. Nat.-Mus. Aschaffenburg, *72*: 38 ♀♂
Ceropales (s. s.) *variegatus:* 1972, WOLF, Insecta Helvetica Fauna: *5* Hym.: 166, 168 ♀♂

Specimens examined: Portugalia: Abrunhosa 31. X. 1944 1♀ NFdANDRADE (Zürich). — Spain: Parade de Rubiales (Salamanca 24. VI. 1961 1♀ on Thapsia villosa v.d. VECHT (Budapest); prov. Bajadoz S. of Monesterio, 700 m 7—8. V. 1960 1♂ Exc. R. M. N. H. (Leiden);? Lerop 12. VIII. 1950 1♂ SANDERS (Leiden). — Italy: Bologna 2. IX. 1962 1♂ (Vienna). — Schwitzerland: Schweiz 1♂ KOHL (Leningrad). — FR Germany: Würzburg 1♀ (Leningrad). — Austria: Umg. Linz 20—21. VIII. 1930 1♂ 2♀ PRIESNER (Vienna); Winden, Bgld. 18. VII. 1963 1♀ PRIESNER (Vienna); Marschtrenk 11. VIII. 1960 1♂ PRIESNER (Vienna). — Hungary: Simontornya 19. VIII. 1929 1♀ PILLICH (Vienna); see MÓCZÁR, 1954 (Budapest) Kecskemét 20. VII. 1962 1♀ BAJÁRI (Budapest); Kelebia 12. IX. 1962 1♂ MÓCZÁR (Budapest); Kéthalom 13. VIII. 1963 1♀ MÓCZÁR (Budapest); Gyula 5—9 .VII., 1—2., 19—20. IX. 1963 11♂ MÓCZÁR (Budapest). — Romania: Agigea 8. VI. 1968. 1♂, 11. IX. 1968. 1♀ 2♂ NAGY (Budapest); Caraorman 24. VIII. 1968. 1♀ NAGY (Budapest). — Russian SSR: (Europe =) Sarepta 1♂ BECKER, 17. VI. 1905 2♀ KOCH (Leningrad); Penza 27—29 VI. 1964 1♀ TSCHEKANOVSKIJ (Leningrad); Mons B. Bogdo Astrachan Gouv. 29. V. 1917 1♂ KUZNETZOV (Leningrad); Gremyatshka, =Grem'acje Dankovsky uezd,

Ryasan Gouv. 28. VII. 1901 1♂1♀ SEMENOV (Leningrad); Orenburg 28. VII. 1922 1♀ (Leningrad); Saratov 9. VI. 1898 3♂ KALKOV (Leningrad); (Asia =) West part of Karsunsky uezd, Simbirsk Gouv. 7. VII. 1964 1♂ TSHEKANOVSKY (Leningrad); Britsh-Mulla 31. VII. 1922 1♀ KUZNETZOV (Leningrad); Iskutsk 1♀ JAKOVLEV (Leningrad); Dar. Kadofbi Konstantinosr. u. Poltavka 1♀ (Leningrad); Pestčanka Troitskosavsk. 10. VII. 1925 1♂ (Leningrad); Spaskoje Orb. okr. (Omszk) 10. VIII. 1930 1♂ RISAKOV (Budapest); Khabarovsk 24. VII. 1925 1♂ ENGELHARDT (Budapest). — Ukrainian SSR: Verhne-Dneprovka Orenb. 20. VII. 1934 1♂ Zimin (Leningrad); Kwiyazh, Kharkov Gouv. 18. VI. 1894 1♂ (Leningrad); Jalta 1♀ (Leningrad); Eupatoria, Krim 1♀ JAKOVLEV (Leningrad). — Georgian SSR: Ladodekhi, Georgia 1—15. V. 1891 1♂ MLOKOSSIEVITSH (Leningrad). — Armenian SSR: 15. V.—15. VII. 1♂ Delitua Armenia (Leningrad). — Azerbaidzhan SSR: Derbent Daghestan 1♂ BECKER (Leningrad); Apsheron, Baku VI. 1963 1♂ GEBEL (Leningrad). — Uzbek SSR: Thimashevo, Samark. 18. VI. 1936 1♀1♂ MELTSHIRENKO (Leningrad). — Tadzhik SSR: Dzhili-Kul. Vaksh, 12—14. VI. 1934 3♂ GUSSAKOVSKIJ (Leningrad). — Kazakh SSR: Uralsk 4. VII. 1927 1♀ RUZAJEV (Leningrad).

The specimens from the above territories correspond to the Central European specimens, only minor colour differences occur e.g. pronotum black (Spaskoje-Omszk, Pestshanka and Hungary: Gyula 1♂) and tergite 1 almost entirely black (Hungary: Gyula 2♂), as well as, spots on tergite 2 remarkably smaller, moreover the right spot on tergite 2 may be missing. Also apical end of abdomen black in the middle (Khabarovsk).

Distribution: Central, East and South Europe, Middle and South Asia.

Ceropales turcomanus GUSSAKOVSKIJ

Ceropales turcomana GUSSAKOVSKIJ, 1926, Revue Russe d'Entom., *20:* 251 ♂
Ceropales turcomana: 1931, GUSSAKOVSKIJ, Ann. Mus. Zool. Acad. Sci. l'URSS., *32:* 4, 14♂

Specimens examined: Turkmen SSR: „Kopet-Dag 29—30. IV. 888 A. P. SEMENOV", „F. MORAVICA", „Ceropales turcomana m. sp. typicum!" with GUSSAKOVSKIJ's original writing and small round, gold-coloured label (Leningrad).

However, in the original description the data of the collecting time and the name are given as 30. IV. 1888 and SEMENOV TIAN—SANSKI, nevertheless, this male specimen without doubt represents the original material and therefore must be regarded as the holotype (Leningrad).

This species is related to *C. variegatus* (FABRICIUS) and to *bicoloripes* MÓCZÁR. *C. turcomanus* distinctly differs from *C. variegatus* (FABRICIUS) in the following characters: postnotum well developed (Fig. 6), medially broadened in a slightly obtuse angle towards propodeum, its surface finely cross-wrinkled and interrupted by a deeper shiny line medially. Mesopleura moderately and sporadically punctured below tegulae. Mesonotum with scattered larger punctures (Fig. 7). Abdomen black, (not rufous) with ivory spots on tergite 1, with narrow apical and in the middle interrupted bands on tergites 2—3, there is small spot also on the right side of tergite 4, with a medial spot on the deeply excised tergite 7, with a continuous apical band on pronotum, etc.

Distribution: Turkmen SSR.

Ceropales bicoloripes MÓCZÁR, **new** ♂

Ceropales bicoloripes MÓCZÁR, 1967, Acta Zool. Acad. Sci. Hung., *13:* 387♀ Fig. 5.

Specimen examined: Russian SSR (Asia =): Blagoveščensk, 22. VII. 1928 1♀ (Budapest). — Turkmen SSR: „Taškepri r. Murgab 12. V. 1954 Tobias" 1♀ (Leningrad), 15. V. 1954 1♂, new (Budapest); Kopet Dag 29—30. IV. 1888 1♀ (Leningrad).

The colouring of this species is not perfectly uniform. The light spots and streaks are smaller and especially reduced on the male specimen. Lateral side of pronotum and mesonotum black; posterior light band of tergite 1 interrupted medially (Turkmen SSR). Hind tibiae and tarsi completely black only under side dark rufous, posterior ends of hind femora distinctly infuscated (Turkmen SSR). Yellow spots on legs very small or partly absent (Blagoveščensk). On the contrary, no black spots present below antennal sockets or on clypeus and the light spots of the invagination of eyes distinctly larger and expanded in a more or less acute angle towards the middle of frons. Also base of mandibles white not black outer orbits on the other hand, more darkened (Turkmen SSR). Sculpturally the frons of holotype (Fig. 10) with a very fine frontal sulcus; specimens from Kopet Dag and from Blagoveščensk also with a shallow deepening round the frontal sulcus. All newly examined specimens with still finer sculptured frons, with more scattered and less shallow larger punctures. Postnotum impressed medially (Fig. 8). Mesonotum with some larger punctures (Fig. 9). Last sternites compressed, produced apically (Fig. 11).

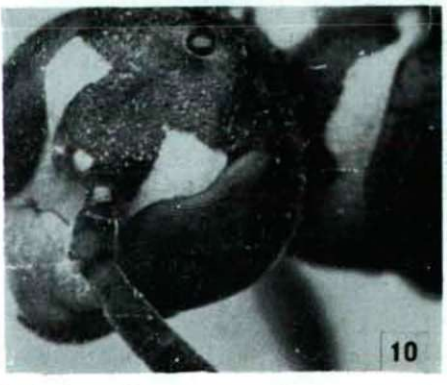
♂. — Length 7 mm. Similar in sculpture and in colour to female. Light colour more reduced, identical with the females described above from Turkmen SSR, differing only in colour of frons and abdomen, light inner edge of spots of frons only obtuse-angled. Band of tergite 1 broader, of tergite 2 only narrow, interrupted, tergite 5 with smaller, 6 with broader lateral spots, tergite 7 white and deeply excised medially. Frontal sulcus very fine, deepening shallow. Punctures of frons very fine, only velvet-like shining, larger shallow punctures can be seen only under greater magnification. This species resembles *C. variegatus* (Fabricius) especially in the single known male specimen of *C. turcomanus* Gussakovskij. Antenna with 13 joints, last tarsal joints of fore legs asymmetric, inner side excised, inner claw very deeply split owing to the unusually large, not truncate inner tooth basally.

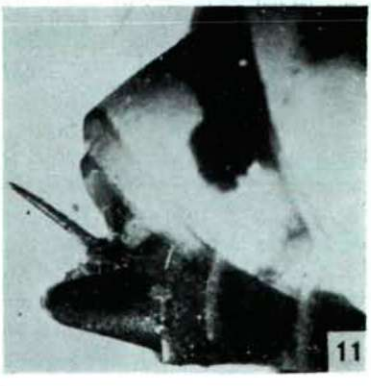
Distribution: Mongolia, Turkmen-, Russian SSR (East Asia).

Ceropales maculatus maculatus (Fabricius)

Evania maculata Fabricius, 1775, Syst. ent.: 345 nr. 108/2
Ceropales maculata: 1931, Gussakovskij, Ann. Mus. Zool. Acad. Sci. l'URSS, *32:* 7, 21♀♂
Ceropales maculatus: 1954, Móczár, Folia Ent. Hung., (S.n.) *7:*148
Ceropales maculata maculata: 1957, Townes, Unit. Stat. Nat. Mus. Bull. *209:* 241 ♀♂
Ceropales (Ceropales) maculatus maculatus: 1965, Wolf, Nachr. Nat.-Mus. Aschaffenburg, H. *72:* 37 ♀♂.
Ceropales maculatus: 1967, Móczár, Acta Zool. Acad. Sci. Hung., *13:* 393 ♂

Specimens examined: Spain: Cataluña 7. 1924. Mas 1♀ de Xarars (Budapest). — France: Cestas, Gironde 7. VI. 1961 1♂ Pronk (Leiden); Haute Marne 2. IX. 1962 1♀ v.d. Vecht (Leiden); Nelik 1♂ Saunders (Leiden). — Netherland: Bildhoven 1. VIII. 1943 1♀ van Ross (Leiden); Rijsplak, Terschelling 14. VII. 1967 1♀ Heijningen (Leiden); Valkenswaard 25. VII. 1945, 25. VIII. 1940 2♀ Blöte (Leiden); Nat. Park: De Hage Veluwe 14. VIII. 1968 1♂ Doeburg (Leiden); Zeist, Uta. 3. VIII. 1952 1♂ de Jong (Leiden); Zundert (N. Br.) 2. VIII. 1957 1♀ Lieftinck (Leiden); Radio Kootwijk 11. VIII. 1946 1♀ on Reseda and Epilobium, v. Rossem (Leiden); Nordberg: Rendkum 24. VIII. 1946, 27. VIII. 1944 2♀ (Leiden); Oisterwijk (N-B) 21. VIII. 1923 1♀ Sonneveldt (Leiden). — Switzerland: Luzern 1. VII. 1♀ (Leningrad). — FR





Figs. 6—7. *Ceropales turcomanus* GUSSAKOVSKIJ, 6 = thorax and tergite 1; 7 = mesonotum. — Figs. 8—11. *C. bicoloripes* MÓCZÁR, 8 = thorax and tergite 1; 9 = pro-, mesonotum-postscutellum; 10 = head; 11 = last abdominal segments (Orig.)

Germany: Würzburg 2♂ 3♀ MORAWITZ (Leningrad); Harz 1♀ 1♂ (Leningrad). — DR Germany: Carolath (Slesien) 2♂ 4♀ MÜLLER (Leningrad). — Austria: Graz 7—16. VII. 1937 1♂ MÉHES (Budapest); Bad Aussee 29. VIII. 1960 1♀ de JONG (Leiden). — Slovakia: Kassa-Bankó (= Košice) VII—VIII. 1939 2♀ 2♂ MÉHES (Budapest); Nyitra (= Nitra) 1887 1♂ MOCSÁRY (Budapest). — Poland: Bielowicza 13. VIII. 1957 1♂ Soós (Budapest); Radoshitsy, Konsky uezd. 24. VII. 1895 1♀ JAKOBSON (Leningrad). — Hungary: see MÓCZÁR, 1954 (Budapest); Kunfehértó 28—31. V. 1962 1♀ 3♂ SOLYMOSNÉ (Budapest); Tompa 11. IX. 1952 1♂ MÓCZÁR (Budapest); Kiskunfélegyháza: Herketó 23. VII. 1962 1♂ MÓCZÁR (Budapest); Kéthalom 13. VIII. 1963 1♂ MÓCZÁR (Budapest); Gyula 30. V., 6., 9. VII. 1963 5♂ MÓCZÁR (Budapest). — Romania: Agigea 18. VII. 1964 1♂ NAGY (Budapest); Hagienidb. 27. VIII. 1968 1♀ NAGY (Budapest). — Yugoslavia: Tetovov, 1800 m 15. VIII. 1963 1♂ (Leiden), — Albania: Ipek 26. VII. 1917 1♀ CSIKI (Budapest). — Italy: Fasana 26. X. 1937 1♀ 1♂ MIJUSSEN (Leiden). — Corse: Bicchisano 2. VII. 1965 1♂ AUBERT (Budapest). — Cyprus: Cherkes 19. VI. 1954 1♀ MAVROMOUSTAKIS (Leiden). — Turkey: Asia. min.: Eski-Tshehir 20. VIII. 1906 1♂ LENDL (Budapest). — Estonian SSR: Glyebova Gorka (= Glybokaja) (= Tartu) 8. VII. 1961 1♂ MORAWITZ (Leningrad). — Russian SSR: (Europe =) Belejev u Szimsz 16. VI. 1907 1♂ GRUGORJEV (Leningrad); st. Hibini Murm. Arhang. (peninsula Kola!) 17. VIII. 1928 1♂ TSHEBUROVA (Budapest); Berditsino, Yarosl. 17. VII. 1896 1♂ YAKOLEV (Leningrad); Yaroslavl', Vertotschi ostr. 27. VI. 1927 1♀, 20. VIII. 1928 1♂ SHESTAKOV (Leningrad); Volozhsk. kraj. Mahtnaja 26. VII. 1933 1♀ (Leningrad); Dnyeprovka 27. VIII. 1934 1♀ (Leningrad); Gremjacka, Dankovsk 17. VI. 1890 1♀, 10. VII. 1912 1♂ (Leningrad); 29. VI. 1890 1♂, SEMENOV (Leningrad); Krasnyj Jar. Astrah. gub. 16. VIII. 1927 1♀ POPOV (Leningrad); Jekaterinoslav 1♂ (Leningrad); Kolomaggi 1♀ MORAWITZ (Leningrad); Dajdarka Kostr. 30. VIII. 1924 1♀, 26. VII. 1935 1♂ GUSSAKOVSKIJ (Leningrad); Vasilevskoje Kostru 21., 24. VII. 1933 3♀ 2♂, 26. VII. 1933 1♂ GUSSAKOVSKIJ (Leningrad); Tverskaya g. Maksatiha 29. VIII. 1926 1♀ SIDORSKIJ (Leningrad); Kostroma 6. VIII. 1933 1♀, 19. VII. 1933 2♀ 3♂ GUSSAKOVSKIJ (Leningrad); Sarepta 16—20. VIII. 1928 1♀ 1♂ Shestakov (Leningrad); Ural protyiv Kharkina 15. VII. 1951 1♀ RUBOLYF (Leningrad); Kyštym Uralsk obl. 27. VIII. 1929. 1♀ BURAKOVA (Leningrad); Sr. Volzhek Kraj. Atsebutik 10. VIII. 1933 1♂ ZIMIN (Budapest); Turgoyak, 1♀ SHESTAKOVO (Leningrad); Mar'ino, Tuapse okr. Tshernom 1♂ SAHNOVSKIJ (Leningrad); Filino-karer 29. VII. 1927 1♀, 1, 6, 31. VIII. 1927 3♀ (Leningrad); ? Disprovska 27. VIII. 1934 1♂ (Leningrad); ? Konetankin 22, 23. 1871 1♂ (Leningrad); ? Silize 3. VII. 1921 1♂ (Leningrad); (Asia =) Padunskaja V. Tunguskye Irk. Tshekanovsk, 500 km N from Irkutsk 1♀ 1♂ (Leningrad); Irkutsk 5♀ (Leningrad); Ot. Kurgana 15. VIII. 1897 1♀ (Leningrad); Minusinsk 1♂ EHENBERG (Leningrad); Ussuri 1♀ KASAKEWITSCH (Budapest); ? Kastrajn 8. VIII. 1923 1♂ GUSSAKOVSKIJ (Budapest); Khabarovsk 15. VII. 1925 1♂ ENGELHARDT (Leningrad); Amurskiÿ okr. Tupidun 2. VIII. 1928 1♂ GUSSAKOVSKIJ; Pestshanka, Troitskosavsk u. Zabajk 20. VII. 1926 1♂ MIHNO (Budapest); Dar. Kadofbi Konstantinosr. 22. VII. 1923 Poltavka 1♂ (Leningrad). — Ukrainian SSR: Vernhe-Dneprovka Orenb. 10, 20. VII. 1934 1♀, 27. VIII. 1934 1♂ ZIMIN (Leningrad); Simferopol 14—15. VI. 1928 2♀ KAZANSKIJ (Leningrad). — Azerbaidzhan SSR: ACCP. Gelachang Zakat 21. VIII. 1928 1♂ BOTSCHARNIKOV (Leningrad). — Tadzhik SSR: Kontdara 1100 m. 7. VIII. 1938 1♀ GUSSAKOVSKIJ (Leningrad). — Kazakh SSR: Borovoe, Kokchetav 3, 22, 24, 26. VII., 7, 22, 24, 26. VII. 1932 12♂ 9♀ POPOV (Leningrad); Pavlodar 27. VII. 1928 1♀ BELIZIN (Budapest); Lebyazhya Petergof. 8. VII. 1899 1♂ (Leningrad); Semipalatinsk 2♀ 5♂ MORAWITZ (Leningrad); Alasanskoe gora VII. 1871 1♂ PRNEVALVEKIJ (Leningrad). — Afganistan: Darnul 3. VIII. 1923 1♂ (Leningrad). — Mongolia: Sutszukte, Kentej 13. VII. 1925 1♀ KOZLOV (Budapest); Khalkha 6. VIII. 1899 1♀ (Leningrad); — Mont. Delgel-Khangai-Ula, Middle Gobi Aimak 25. VII. 1967 1♀ ZAITZEV (Leningrad); 80 km SSE from Nomgon, Bordzan-Gobi, South Gobi Aimak, 5—8. VIII. 1967 1♀ ZAITZEV (Leningrad). — China: Kansu, Nan-piu (Budapest).

The variability in colour and in sculpture of this species is similar to other European and Asiatic specimens. Several female specimens have a small yellow spot on tergite 4 in the middle. The distal end of femora 3 partly darker on the smaller male at the outer side (e. g. Kostroma, RSSR) or dark fuscous not only on both ends of femora 3 but dark fuscous nearly also on the apical half (e. g. Pestshanka, RSSR). The light spots are remarkably smaller also on the smaller specimens (♀♂). Sometimes the lateral spots of tergite 1 are remarkably small and the apical band is also broken medially (♂) (e.g. Kastrajn, RSSR). Exceptionally a female specimen from Mongolia (Sutszukte) has two slightly extended light spots towards the middle

of tergite 1 connected with a rufous band. The two lateral spots may extend towards the middle of tergite 1 to such a degree, that they nearly fuse (e.g. Turgoyak, RSSR), or in fact completely fuse (e.g. Pavlodar ♀, Kazakh SSR). This extreme form with a yellow band on tergite 1 was described as var. or subsp. *flavopicta* by GUSSAKOVSKIJ in 1931 from Mongolia. Its sculpture is remarkably finer especially on the propodeum of the smaller male specimens (e.g. Kostroma RSSR) and in contrary there are also smaller male specimens (Hungary: Kunfehértó, Tompa, Gyula) with more coarse sculpture. Posterior margin of tergite 1 of a specimen from China brownish behind the yellow band; after all the light colour of the body, except legs not pure white, rather yellowish.

Distribution: Europe, from peninsula Kola to North Africa and Asia to Mongolia, to Armenian-, Azerbaidzhan-, Tadzhik-, Kazakh-SSR, Afganistan, China and Japan.

Ceropales maculatus maior COSTA

Ceropales maculata var. *maior* COSTA, 1888, Atti. Accad. Sci. fis. mat. Napoli, *2:* 11
Ceropales maculatus maior: 1975, WOLF, Zool. Mededel., *49:* 48♀

Specimen examined: Portugal: Douro-Resende 16—19. VII. 1959 1♀ PMF VERHOEFF (Zürich). — Spain: Mallorca 1.24. VI. 1954 1♀ KLOKKE-MOLL (Budapest). — Turkmen SSR: Čili, Kopet-Dag, Zakasp obl. 3. VI. 1914 2♀ GOLBEK (Budapest, Leningrad); the same data, but 6—8. V. 1913 1♀ (Leningrad); Kara-Kala 12. VI. 1952 1♀ KRYZHANOVSKIJ (Budapest).

This subspecies is characterized on the basis of the above listed specimens especially by the almost entirely black femora, by the small or very small ivory spots of tergite 1, by the remarkably narrow apical ivory band of tergite 2, by the normal medial spots on tergites 5 and 6. Clypeus usually with two small ivory spots laterally. The light spots sometimes slightly yellowish. The colouring is not completely uniform. Under the edge of femora 3 on a Portugese specimen surface rufous, pronotum without a light apical band on a specimen from Spain, the apical band interrupted on specimen from Portugal. One of the specimens from Kopet-Dag with a very small light band medially on tergite 4. The single difference is that tibiae and tarsi rufous on specimens from Turkmen SSR, but the same are fuscous to a great extent on specimens from Portugal and Spain. Completely black tergite 1, described by COSTA from Sicily, is not found on specimens originating from Portugal or Spain nor on those from Turkmen SSR. In spite of these differences and the great distance between their known localities I suggest that all these specimens be regarded as the same subspecies.

Distribution: South Europe, Turkmen SSR.

Ceropales maculatus turcmenensis subsp. n.

♂. — Similar to *maculatus maculatus* FABRICIUS, 1775, but differs from it as follows: femora black and only apically rufous, tergite 4 with rudimentary white apical band, tergites 5—6 with narrow apical band, tergite 7 with two lateral spots. Yellow longitudinal streak below antennal sockets only on specimen from Kara-Kala. Near to *C. maculatus caenosus* TOWNES, 1957, but light spots white not clear yellow and mesopleuron black, without a small clear yellow spot. Holotype with

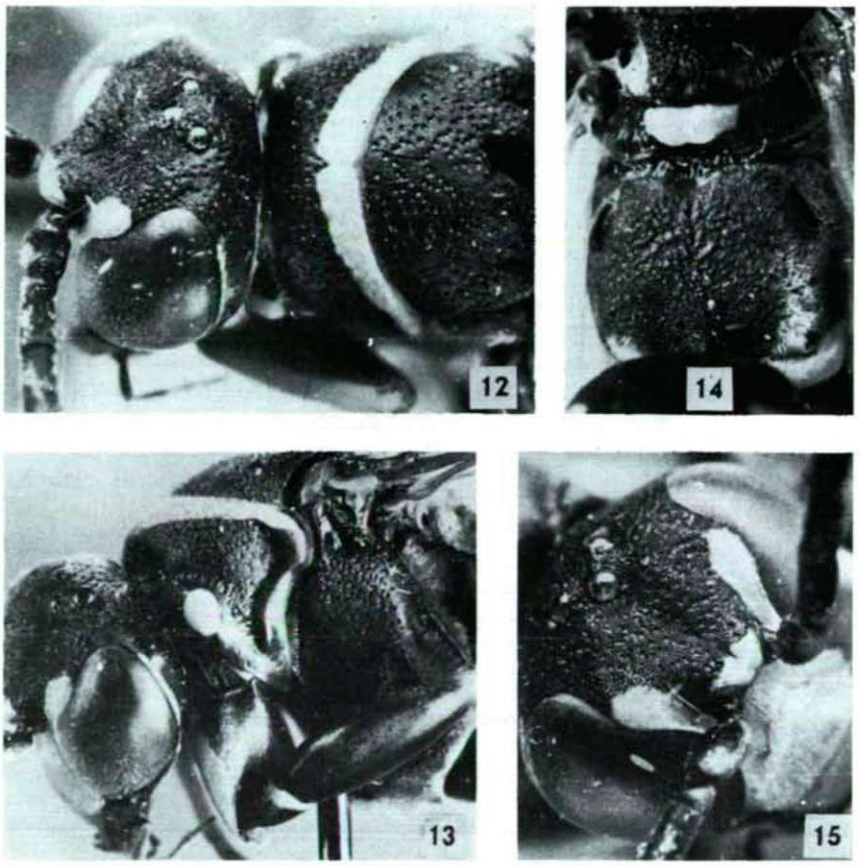
a distinct longitudinal sulcus at base of propodeum medially, paratype only with trace of that. Sculpture of propodeum only somewhat coarser than on *C. maculatus maculatus* FABRICIUS.

Specimens examined: Turkmen SSR: "Bagir (Ashabad) 21—23. IV. 929 A. SHESTAKOV", "*Ceropales maculata* FB. V. GUSSAKOVSKIJ det." 1♂ holotype Hym. Typ. No 3643 (Budapest); "Bagir (Ashabad) 21—23. IV. 929 A. SHESTAKOV", "k. SHESTAKOVA" 1♂ paratype (Leningrad); Kara-Kala, 26. VI. 1952 1♂ BORISOVA (Budapest).

Ceropales magnificus GUSSAKOVSKIJ

Ceropales magnifica GUSSAKOVSKIJ, 1926, Revue Russe d'Entom., *20*:252♂
Ceropales magnifica: 1931, GUSSAKOVSKIJ, Ann. Mus. Zoll. Acad. Sci. l'URSS, *32*:22♂

Specimen examined: Russian SSR: "St. Imanpo, Mandsuria, 18. VII. 1914 EMELJANOV", a small rounded golden coloured label, "*Ceropales magnifica* n. sp." in GUSSAKOVSKIJ's original writing (Leningrad).



Figs. 12—15. *Ceropales magnificus* GUSSAKOVSKIJ, 12=head, pro- and mesonotum viewed from above; 13=the same in lateral view; 14=scutellum — propodeum; 15=head (Orig.)

It corresponds with the original description, therefore must be regarded as the holotype of this species. The species is a relative of *C. maculatus maculatus* (FABRICIUS), but frons with some distinct larger punctures (Fig. 15), pronotum with apical yellow band and with a small hyaline margin (Fig. 12—13). Light colour of body yellow, tergite 3, as well as, femora 3 mostly black. Sculpture especially on propodeum distinctly coarser (Fig. 14) than on *maculatus maculatus* (FABRICIUS). Mesonotum, mesopleura with deep scattered punctures.

Distribution: Russian SSR: Manchuria.

Ceropales altaicus F. MORAWITZ

Ceropales altaica F. MORAWITZ, 1888, Trudy russk. ent. Obshch., *22*:272 ♂
Ceropales altaica: 1931, GUSSAKOVSKIJ, Ann. Mus. Zool. Acad. Sci. l'URSS, *32*:20 ♂

Specimen examined: Kazakh SSR: "M. Kolbinsky, Sentasch-Piket", a small round and gold-coloured label, "k. F. MORAWITZ", "altaica F. MOR. ♂" with MORAWITZ's hand writing, 1 ♂ (Leningrad); the some locality and "*Ceropales altaica* ♂ F. MORAWITZ" 1 ♂ (Budapest).

They represent the original material, therefore the first can be regarded as lectotype the second one as paralectotype (Hym. Typ. No. 3644, Budapest). According to MORAWITZ: "Sentasch ist ein Wachposten in den kolbinskischen Bergen, den Süd-Ausläuferen des Altai, Terr. Semipalatinsk."

It is a very charakteristic species with rich yellow colour: frons largely, whole pronotum, metapleura with two spots (Fig. 16—17), tergites 1—2 with yellow broader than their half, legs largely yellowish rufous, etc. Propodeum mat, granulated, with wrinkles directed to the base of abdomen and with two lateral distinct ridge arching towards stigma (Fig. 18). Last sternites: Fig. 19.

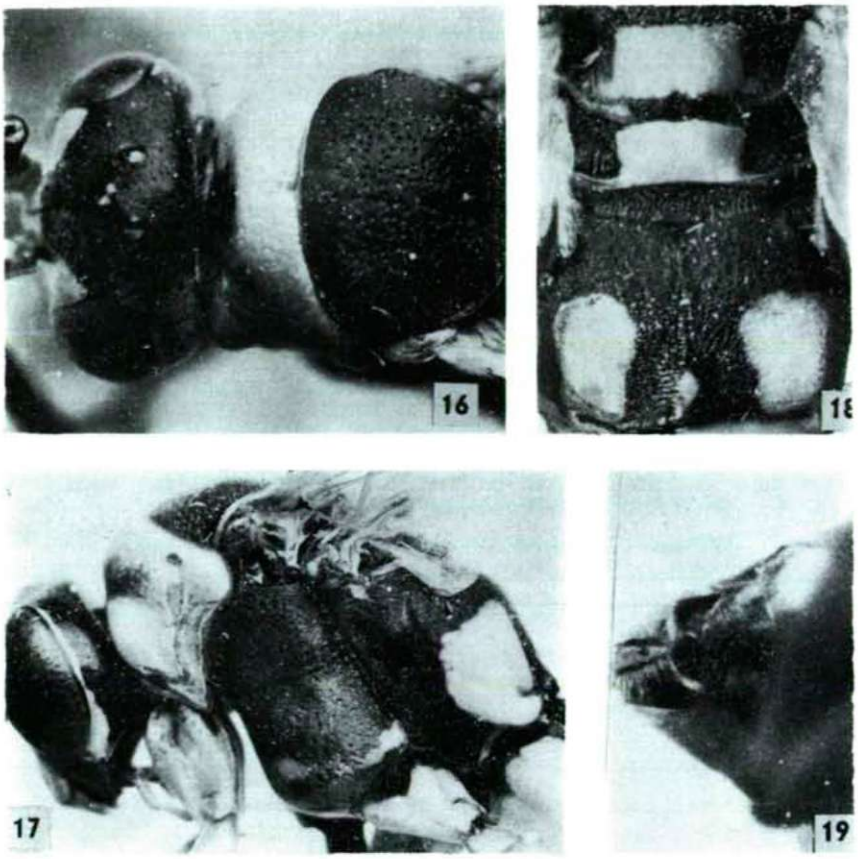
Distribution: South middle part of Russian SSR.

Ceropales sibiricus RADOSZKOWSKI

Ceropales sibiricus RADOSZKOVSKI, 1888, Bull. Soc. nat. Moscou, *2*:490 ♀♂
Ceropales sibirica: 1926, GUSSAKOVSKIJ, Rev. Russ. d'Entom. Leningrad, *20*:254♀♂
Ceropales latitarsis HAUPT, 1938, Arkiv för Zoologie, *30A*: 13♀♂ Fig. 5—6
Ceropales sibiricus: 1977, MÓCZÁR, Ann. Hist,-nat. Mus. Nat. Hung., *69*:255♀♂ Taf. I. Fig. 4, Taf. II. Fig. 3—4.

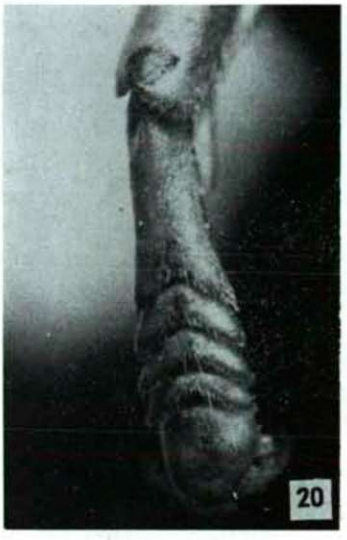
Specimens examined: Russian SSR: (Asia=): "Minusinsk Ongudai 1♂" (Leningrad); Ongudai, Bijsk Mont. Tomsk Gouv. 8. V. 1929 2♂ JAKOBSON (Leningrad); Transbaikal, Čita 1♀ (Budapest); Čita-Motschun 1♀ KOBYDEV (Leningrad); Gusinoje, Selenginsk u. Zab. Mihno 21—22. VII. 1927 1♀ 2♂ TSHOGANNOR (Leningrad); Enisey. Gouv. Imek 1♀ JAKOBSON (Budapest); Khabarovsk 15. VII. 1926 1♀ (Leningrad); Razyezd, Soktui, Nertshinsk uezd Transbaikal 7—23. VI. 1925 5♀ 8♂ VINOGRADOV (Leningrad); Selenga, Zaruvinye, Zabajk 26—27. VI. 1928 1♀ (Leningrad); ? Mandeina 1♀ GUSSAKOVSKIJ (Budapest); Osnatjenn 1♀ EHNBERG (Leningrad). — MONGOLIA: Dol. r. Tolü, Khalkha 20. VI. 1925 1♂ (Leningrad); Kholt sev. Gobi 16. VI. 1926 1♀ 1♂, 14. VII. 1926 1♀ 1♂, 15—19. VII. 1926 1♂ KOZLOV (Leningrad); Bain-Baritye 11. VI. 1909 1♀ 1♂ KOZLOV (Leningrad); Sarhaj-hunduj, Halha 24. VII. 1909 2♀ (Budapest, Leningrad); Ceorgolhairhan, Halha 23. VII. 1909 1♂ KOZLOV (Budapest); Lamin, Hangaj 18. VII. 1926 1♂ KIRITSHENKO (Budapest) 1♂ (Leningrad); N. Mongolei 1892 1♂ 1♀ LEDER (Vienna); 103 ♀♂ (see MÓCZÁR 1977).

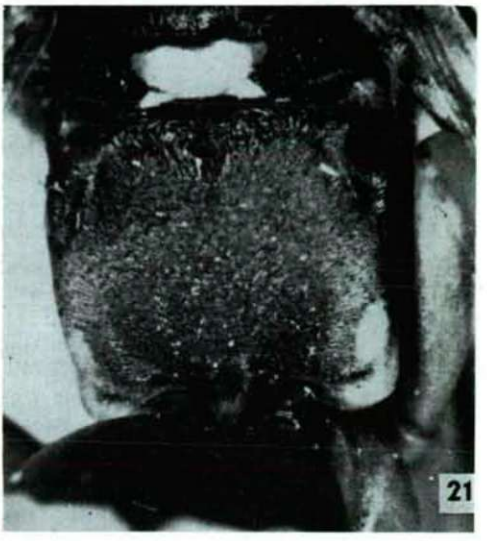
In the original description the holotype was not designated, only the locality was given "Sibérie (Kultuk, Minousinsk)", therefore I suggest to regard this speciemen



Figs. 16—19. *Ceropales altaicus* F. MORAWITZ, 16 = head, pro- and mesonotum viewed from above; 17 = the same in lateral view; 18 = scutellum — propodeum; 19 = last abdominal sternites (Orig.)

from Minusinsk as the lectotype (Leningrad). On the basis of 123 ♀♂ examined specimens the species seems to be variable especially in colour. Sometimes the continuous black streak between the antennal sockets and the lower margin of labrum narrowly yellowish interrupted (♀♂). This charakter represents an advance to *C. andersoni* HAUPT, 1938, howewer, frons black above the antennal sockets, consequently, these specimens cannot be *C. andersoni* HAUPT. Sometimes darker ferruginous small margins appear above the lateral yellow spots on propodeum (Zaruvinye, RSSR) or dark ferrugineous and transparent band connect the lateral apical bands of tergite 1 (Kholt sev. Gobi, Mongolia). Sometimes the lateral yellow spots of propodeum are missing on the smaller specimens (Georgol-hairhan, Mongolia, Transbaikalia, Russian SSR). RADOSZKOWSKI did not give in his diagnosis the very broad fore tarsi (Fig. 20), therefore had been described by HAUPT as *C. latitarsis* sp. n. in the earlier material I too misidentified this species (MÓCZÁR





Figs. 20. Fore tarsal joints of *Ceropales sibiricus* RADOSZKOWSKI, ♂. — Fig. 21. Postscutellum-propodeum of *C. erythropodus* GUSSAKOVSKIJ (Orig.)

1977). There is no doubt about it, that the HAUPT's Figs. 5—6 of *latitarsis* HAUPT entirely correspond to *C. sibiricus* RADOSZKOWSKI.

Distribution: Asia, Russian SSR, Mongolei.

Ceropales ruficornis ruficornis GUSSAKOVSKIJ **stat. n.**

Ceropales ruficornis GUSSAKOVSKIJ, 1931, Ann. Mus. Zool. Acad. Sci. l'URSS, *32*:12 ♀♂

Specimens examined: Russian SSR: (Asia—SE from Baical): "ACCP Altan 20. VI. 1927 I ZAPOLSKY" "k. GUSSAKOVSKOGO" 1♂ (Leningrad). — Azerbaidzhan SSR: "Kurutshaj 2. VI. 1927 GUSSAKOVSKIJ", "*Ceropales ruficornis* m. ♂ specimen typicum V. GUSSAKOVSKIJ det." with author's hand writing, "k. GUSSAKOVSKOGO" 1♂ (Budapest); without locality label, but with GUSSAKOVSKIJ's original det. label: "*Ceropales ruficornis* m. ♀ sp. typicum GUSSAKOVSKIJ" 1♀ (Leningrad). — Turkmen SSR: Iman-baba 1932 SHESTAKOV 1♂ (Budapest). — Cyprus: Zakaki VII. 1936 1♀ (Budapest); Zakaki VIII. 1935 1♂ (Budapest).

In the original description the holotype was not designated, it was given only "Azerbaidzhan, sz. Altan, VI. 1927 2♂", therefore, I suggest the one ♂ from Altan on the basis of the original material as lectotype and the other ♂ specimen from Kuru-tschaj = Kuručay as paralectotype (Hym. Typ. No. 3645, Budapest) (also from Azerbaidzhan and also with the same data of collecting time), on the basis of GUSSAKOVSKIJ's original writing in spite of the fact, that the nearer locality Kuručay of the second male was not designated by GUSSAKOVSKIJ.

The species is easily recognizable since all the tergites are marked with yellow bands, by the normal tarsi 1—2, by the large yellow spot extending between inner orbits from antennal sockets nearly to lower ocellus, by the coarsely rugose propodeum, by the rich yellow coloured body. Since the species is closely related to

C. gilvus HAUPT, 1962, I suggest to regard it as *C. ruficornis* subspecies *ruficornis* GUSSAKOVSKIJ.

Distribution: Russian- (Asia), Azerbaidzhan-, Turkmen SSR and Cyprus.

Ceropales ruficornis gilvus HAUPT **stat. n.**

Ceropales gilvus HAUPT, 1962, Bull. Res. Counc. of. Israel, *11B* (1—2): 32 ♀♂
Ceropales gilvus: 1966, PRIESNER, Israel Journ. Ent., *1:* 151—152 ♂

Specimens examined: Palestine: "Jerusalem 12. VI. 1941 BYTINSKI-SALZ" 1♀ (Hym. Typ. No. 3646, Budapest); Jerusalem 29. V. 1941 BYTINSKI-SALZ 1♂ (Vienna).

The first specimen is one of the paratypes, because the collecting data and the locality agree with HAUPT's diagnosis and the female specimen was identified by the author in 1952 according to the HAUPT's det. label with HAUPT's hand writing. This species is very similar to *C. ruficornis* GUSSAKOVSKIJ especially to the specimen without locality label but which was identified by GUSSAKOVSKIJ (see above). The very minute differences are as follows: on paratype of *C. gilvus* (♀) we cannot find the black streak on tergite 1 medially which broadly ends before posterior margin on *ruficornis*; the yellow bands on tergites 2—3 on *gilvus* (♀) distinctly broader than on *ruficornis*; the minute black line is present only on *gilvus* (♀) in the middle of frons above the antennal sockets; on *gilvus* (♀♂) there is also a very small yellow spot in the angle between tegulae and pronotum; the middle of the pronotum broadly impressed on *ruficornis* and narrowly on *gilvus,* the latter similar to the female from Cyprus, on which the colouring distinctly retired. It may be possible, that *gilvus* HAUPT will prove to be a synonym of *ruficornis* GUSSAKOVSKIJ after the examination of the holotype (♀) and also the designated other paratypes (♀♀ ♂♂) given by HAUPT in his description. In the meantime I propose to treat this taxon only as a subspecies.

Distribution: Palestine.

Ceropales solskyi RADOSZKOWSKI

Ceropales Solskyi RADOSZKOWSKI, 1877, in FEDCENKO: Puteš. Turkes. *14.* II. Zoogeogr. Isl. V. *3.* Sphegidae: 13 ♂ n. 1. Tab. VI. Fig. 8 ♂
Ceropales solskyi: 1931, GUSSAKOVSKIJ, Ann. Mus. Zool. Acad. Sci. l'USSR, 32:17 ♀♂

Specimens examined: Tadzhik SSR: Kalai—Vamar, Roman. v Buchara (=Rušhan), Lazdin 14. VII. 1915 1♀ (Budapest); ur. Rujdasty 3000 m 40 km N. Stalinb. 4. IX. 1937 2♂ (Budapest), 1♀ 2♂ (Leningrad).

This species was described from Ferghana (10. Aug. 1871), it is easily recognizable also by tergites 3—4 with their apical light band, by the normal tarsi 1—2 (♀ ♂), by the broad black streak running from ocellus to the lower margin of clypeus, by the mostly yellow-black legs, by the rich yellow coloured tergite 1 which is connected with the rough surface of propodeum, etc.

Distribution: Uzbek-, Turkmen — and Tadzhik SSR.

Ceropales trjapitzini sp. n.

♀. — Length 9 mm. Black. Inner orbits beginning at excision of eyes (Fig. 22) and broadening towards clypeus, tubercle between antennal sockets, under side of antennal joints 1—2, transverse streak along the margin of clypeus, clypeus and labrum except a small round black spot medially, a very small streak on upper-outer eye margin, a rather broad hind margin of pronotum (Fig. 23), narrow only laterally, a spot on front callus of pronotum (Fig. 23), on postcutellum and on propodeum laterally (Fig. 24), whole horizontal level of tergite 1 except hind narrow black margin, a broad band on tergites 2—6, lateral spots on sternites 2 and 4, ventral side of coxae, a small streak on trochanters distally, apical half of fore femora at outer side, nearly whole outer side of middle femora, a longitudinal streak on upper side and apex of hind femora, all tibiae except outer black and partly rufous apex of hind ones, metatarsi and tarsal joints partly, yellow; apex of mandibles, ventral side of tergite 1 laterally partly, inner side of fore and middle femora, as well as, outer side along black spot of hind ones and tarsal joints partly rufous. Pterostigma of fore wings brown. Frons with dense minute punctures and also with scattered larger punctures (Fig. 22), mesonotum (Fig. 24—25) and mesopleura with deep and dense punctures (Fig. 23), scutellum with longitudinal sulcus medially, postscutellum impressed medially, postnotum rather broad and irregularly wrikled except a small polished spot in the middle before propodeum (Fig. 24), latter irregularly and rather coarsely rugose, gradually convex on its basal third, flat in apical two-thirds, last abdominal sternite with a projecting apical part whose apex truncate in profile. Longer hairs of frons erect, rather short and sparse.

♂. — Length 10 mm. Similar to female, but whole lower face (= below antennal sockets) yellow, scutellum also with a transversal yellow streak, hind black margin of tergite 1 broader, tergite 3 black only with a small transversal yellow streak posteriorly, tergite 7 yellow, last sternite not projecting, subgenital plate broadly truncated apically, second to fourth joints of fore tarsi about as long as wide, second joint of middle ones twice as long as wide.

Specimens examined: Tadzhik SSR: "ur. Rujdast'y 3000 m. 40 km N. Stalinb. 4. IX. 37. GUSSAKOVSKIJ", "K. GUSSAKOVSKAVA" 1♀ holotype (Leningrad) and 1♂ allotype Hym. Typ. No. 3647 (Budapest).

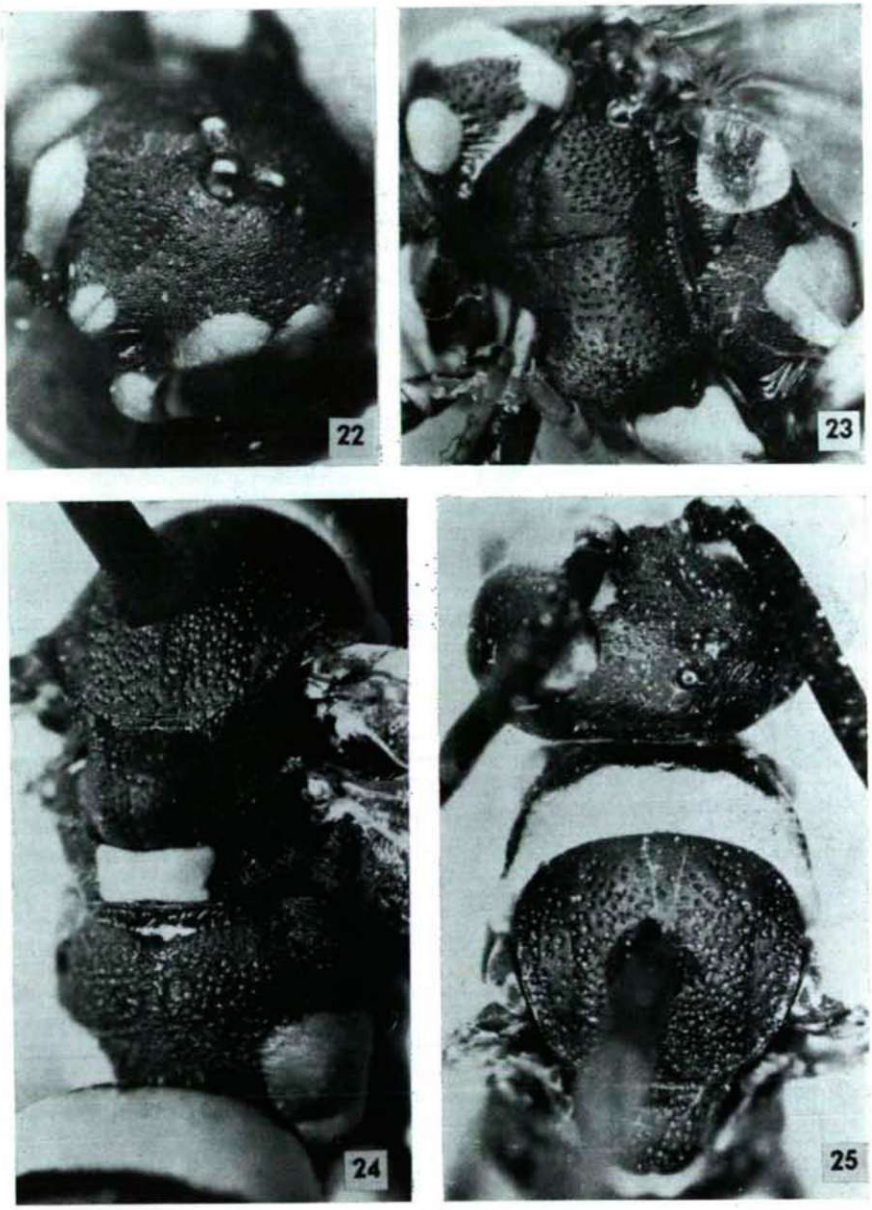
Related to *solskyi* RADOSZKOVSKI, but differs chiefly as follows: propodeum not irregularly wrinkled, not only finely transversally wrinkled, yellow spots on pronotum and on body not smaller, yellow spots of tergite 1 not connected, etc.

I have named this species in honour of the excellent Russian specialist of Chalcidoidea, V. A. TRJAPITZIN (Leningrad).

Ceropales erythropodus GUSSAKOVSKIJ

Ceropales erythropoda GUSSAKOVSKIJ, 1926, Revue Russe d'Entom., *20*:253♀♂
Ceropales erythropoda: 1931, GUSSAKOVSKIJ, Ann. Mus. Zool. Acad. Sci. l'URSS, *32*: 7, 19♀♂
Ceropales erythropodus: 1977, MÓCZÁR, Ann. Hist.-nat. Mus. Nat., Hung. *69*:256♀♂ Taf. I. Fig. 1—3.

Specimens examined: Turkmen SSR: "Turkestan", a small round gold coloured label, "k. A. JAKOVLEVA", "*Ceropales erythropoda* m. V. GUSSAKOVSKIJ" with author's original writing, 1♀ (Budapest). — Russian SSR (Asia=): "Minusinsk, Eniseish gub. Yu. Vagner 21. VII.



Figs. 22—25. *Ceropales trjapizini* sp. n., 22 = head (allotype); 23 = thorax in lateral view (allotype); 24 = thorax and tergite 1 (holotype); 25 = head and thorax viewed from above (holotype) (Orig.)

1897" (not 26 as in the diagnose), a small round gold label 1♂ (Leningrad); Gusinoje Selenginsk. u. Zab. Mihno 21—22. VII. 1927 1♂ (Leningrad); "Stantion Malta, Sibirishe Eisenbahn, Irkutsk Gav. 22. VI. 1907 leg. D. SMIRNOV", "*erythropoda* m. V. GUSSAKOVSKIJ", a small round gold label, 1♀ (Leningrad); "Ufer von Fluss Katun, Süd Altai 20. VI. 1898 leg. KLEMENTZ", a small round gold label 1♀ (Leningrad); Nertčinsk, South Siber. 25. VIII. 1910 1♂ RUDNITZKAYA (Leningrad); Balsino Čita uezd, Transbaikal, South Siber. 1. VIII. 1925 1♀ 1♂, VINOGRADOV (Leningrad). — Mongolia: "Sangin, Urga s. Mongolia, KOZLOV, 26. VII. 1905", a small round gold coloured label, 1♀ (Leningrad); "r. Tola Urga, s. Mongolia, KOZLOV, 11—12. VII. 1905", "*Ceropales erythropoda* m. GUSSAKOVSKIJ with author's hand writing, a small round gold coloured label, 1♂ (Leningrad); "r. Tola Urga, s. Mongolia, KOZLOV, 9—10. VII. 05", a small round gold label, no more label, 1♂ (Budapest); "okr. Urga, s. Mongolia, KOZLOV 5—7. VII. 05", a small round gold label, no more label 1♂ (Leningrad); Kholt sev. Gobi 14. VII. 1926 1♂ KOZLOV (Leningrad); Dol. r. Tolü Khalkha 1—10. VII. 1926 1♂ KOZLOV (Leningrad); N. Mongolei 1892 1♀ LEDER (*sibirica* det. KOHL) (Budapest); Tuin-gol, Khalkha, 29. VI. 1926 1♂ KIRITSHENKO (Leningrad); Lamingegen, Hangaj 9., 18., 27. VII. 1926 1♀ KIRITSHENKO (Budapest) 3♂ (Leningrad); Sarhaj-Hunduj, Khalkha 24. VII. 1909 KOZLOV 1♂ (Budapest). — China: Harbin (=Mandsuria) 25. VI. 1950 1♀ ALIN (Zürich).

Among the specimens examined there are some which represent the original material, GUSSAKOVSKIJ did not designate the type-specimens, therefore I suggest the first specimen with exact data "Minusinsk" as lectotype (Leningrad), the following specimens as paralectotypes: "okr. Urga" with Hym. Typ. No. as follows: "Turkestan" No. 3648 (Budapest); "Sangin" (Leningrad), "Tola Urga" 9—10. VII. 05, No. 3649 (Budapest); "Tola Urga" 11—12. VII. 05 (Leningrad).

This species resembles *C. maculatus maculatus* (FABRICIUS) owing to the sculpture of propodeum, but frons with more or less distinct and larger, scattered punctures. It is characterized by the light yellowish rufous legs, by the ivory spots on tergite 1 and by the narrow ivory apical bands of tergites 2—6(7), by the normal, not dilated tarsi, by the black streak of frons clypeus medially (♀), and by the slightly rough wrinkled surface of the propodeum (Fig. 21). Mesopleura and tergite 1 on specimen from Turkmen SSR partly with rufous spots.

Distribution: Mongolia, Turkmen-, Russian SSR (Asia=) and China.

Ceropales albicinctus albicinctus (ROSSI)

Evania albicincta ROSSI, 1970, Faun. Etrusca, *2*:57 nr. 800 T. 6. F. 8
Ceropales albicincta: 1931, GUSSAKOVSKIJ, Ann. Mus. Zool. Acad. Sci. l'URSS, *32*:5, 13♀♂
Ceropales albicinctus: 1947, BEAUMONT, Mitt. Schweiz. Ent. Ges., *20*:506, 515♀♂
Ceropales albicinctus: 1954, MÓCZÁR, Folia Ent. Hung., (S. n.) *7*: 149
Ceropales albicinctus albicinctus: 1969, PRIESNER, Naturkundl. Jb. Linz *115*, 119 ♀♂
Ceropales (s. s) *albicinctus:* 1972, WOLF, Insecta Helvetica Fauna *5* Hym.: 1968., 69 ♀♂ Fig. 489♂

Specimens examined: Switzerland: Schweiz VIII. 1883 2♀ KOHL (Vienna); Vallis, Misox (WOLF, 1972). — Italy: Pisa, Casciana terme 15—25. VII. 1963 1♀, 1—15. VIII. 1965 1♂ (Vienna); San Remo 1♀ (Budapest); Bozen 1893 1♂ KOHL (Budapest); Bologna 2. IX. 1962 1♂ (Vienna). — Austria: Pulgarn 2. IX. 1959 1♀ PRIESNER (Vienna); Ober Weiden 1♂1♀ MADER (Vienna); Eichkogel 8. VIII. 1909 1♀ RUSCHKA (Vienna). — Hungary: Simontornya 29. VI. 1931 1♀ on Enphorb. gerard. PILLICH (Vienna); Ungarn 1884 1♀ KOHL (Vienna); see MÓCZÁR, 1954 (Budapest); Gyula: Pósteleki e. 9. VII. 1963 2♀8♂ MÓCZÁR (Budapest). — Yugoslavia: Insl. Krk 2♀ MADER (Vienna). — Graecia: Tolon 17. VI. 1966 1♀ SCHLÄFLE (sabulicola PR. det. WOLF) (Budapest); Corfu 1♀ PAGANETTI (Budapest). Turkey: Erdschias 14. VII. 1♂ PENTHER (Budapest). — Jordan: Jericho 1900 1♂ SCHMIEDEKNECHT (Budapest). — Russian SSR: (Europe=) Kilintshi okr. Astrahan 25. V. 1930♂ OGLOBLIK (Leningrad); Temirchan-Shure (Dagest), 1♂ (Leningrad); Sochi 16—27. sen. 1926 4♀ 3♂ (Leningrad); 1♀1♂ (Budapest); Sarepta 6. 10. VI. 1907 3♂, 4♂5♀ BECKER, 13—23. VI. 1909 2♂7♀ KOCH, 3♀, 23—26. VIII. 1926 2♂ SHESTAKOV (Leningrad), 1♀1♂ (Budapest); okr. Krasnodar 12. IX. 1927 1♂ TELENGA (Leningrad); Woronesh 1♀ (Leningrad); Petrovskoe Staurop. okr. 3. IX. 1927 2♂ BELIZIN (Leningrad);

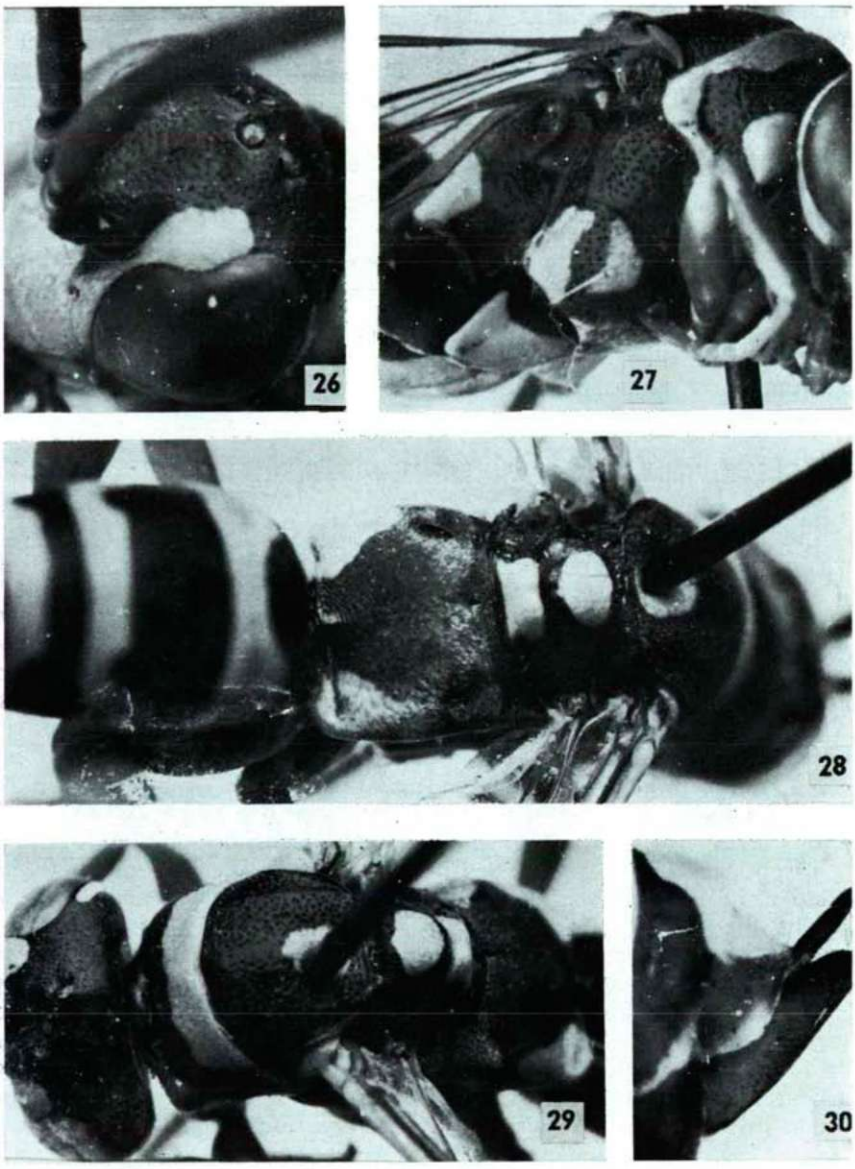
Concess. Krupp. Salks region, North Caucasus 3. VIII. 1931 1♂ ROHDENDORF (Budapest); okr. Orenburga 9. VIII. 1927 1♂ 27. VI. 1926 1♂ VORONTSOVSKI (Leningrad); (Asia=) Kongrad 1. VIII. 1923 1♀ POLTOVEK (Leningrad); Razyezd Soktui, Nertshinsk uezd Transbaikal, South Siber. 17. VI. 1929 1♂ VINOGRADOV (Leningrad); Prikumsk Krasnod. kraj 27. VI. 1926 1♀ PATIKTSA (Leningrad). — Moldavian SSR: Kotushep, Leovo Bendery uezd, Bessarabia 15. VII. 1911 1♂ TSHERMAVIN (Leningrad). — Ukrainian SSR: Kerč 3. V. 1906 1♀ (Leningrad); Saki, Krim, Tauria 30. VII.—10. VIII. 1913 4♂ PLIGINSKI (Leningrad); Simferopol 28. V. 1900 1♀ 10., 14., 24. VI. 1928 1♀1♂ KAZANSKIJ (Leningrad). — Georgian SSR: Tiflis 22. VII. 1901 1♂ SATUNIN (Leningrad). — Armenian SSR: Kaukazus Araxesthal 1♂ LEDER (Leningrad) Martuni 19. IX. 1927 1♂ KONSTANDYAN (Leningrad); Transkauk. 1886 1♀ HELENENDORF (Vienna). — Azerbaidzhan SSR: ACCP Kuduly Nuch. u. 29. VI. 1928 1♂ BOTSHARNIKOV (Leningrad); ACCP Tasbulah 19. VI. 1928 1♂ BOTSHARNIKOV (Leningrad). — Kazakh SSR: Semipalatinsk 1♂2♀ (Leningrad); okr. Uralska 15. VII. 1907 1♂ (Leningrad), 1♂ (Budapest); Uralsk 1♂ BARTEL (Vienna); Ber. Tschogur Mugodjarg. 26. VI. 1910 1♀1♂ (Leningrad); Ryn-Pesski 1♂ (Leningrad). — Japan (WOLF, 1972). (Fig. 37).

The species is easily recognizable by the propodeum with its fine sculpture weakly shining, by the silvery pubescence, by the narrow ivory apical bands of all tergites (except 1 very small ♂ from Sarepta and 1 ♂ from Krim, where tergites 1—6 interrupted and except males from Azerbaidzhan, where tergite 5 is black without ivory band and where the extent of ivory yellowish colour is small), by the ivory lower face and by the light rufous legs as well as the under side of antennae which are dark rufous on the upper side and infuscated at the end joints of specimen from ACCP Kuduly. The apical part of hind tibia (♀ ♂) more or less brownish darkened, as well as, hind tarsal joints and last tarsal joint of middle tarsi from Europaean territories; hind tibia largely black on a female specimen from Greece, and on males from Hungary (Gyula); more rufous and less infuscated on specimens from Sochi, Sarepta, Simferopol, lastly the above mentioned parts completely rufous and not darkened on specimens from Sochi, Sarepta and from Kongrad and Prikumsk.

Distribution: Central and partly South Europe, Russian-, Ukrainian-, Georgian-, Armenian-, Azerbaidzhan- and Kazakh SSR, Japan.

Ceropales albicinctus wolfi ssp. n.

♀. — Length 10,5 mm. Black. Inner orbits beginning at emargination of eyes with a large rounded spot (Fig. 26) outer orbits, lower side of tubercle between antennal sockets continuing in a triangular spot of lower face medially, clypeus, labrum, mandibles, a spot on lower side of antennal joints 1—2, posterior and lateral margin of pronotum, a spot on front callus of pronotum (Fig. 27), as well as, on mesonotum, scutellum and postscutellum, lateral spots on propodeum (Fig. 28), a large triangular and smaller semicircular spot on mesopleura below (Fig. 27), a broadely emarginate posterior band of tergite 1, posterior and lateral distinctly emarginated bands on tergites 2—4, bands broadened laterally especially on 2nd (Fig. 28), large medial spots on tergites 5—6, small round spots on sternites 2—5 laterally, apical small streak on trochanters, lower side of coxae except hind ones, latter with a triangular black spot, outer apical large spots on all femora; outer basal and apical spots on fore and middle tibia, as well as, on outer basis of hind one, ivory. Under side of antennal joints 3—12, apex of mandibles, apical two-thirds of trochanters, femora, tibia and tarsi except ivory spots, rufous; outer apex



Figs. 26—30. *Ceropales albicinctus wolfi* ssp. n., 26=head; 27=thorax in lateral view; 28=thorax and abdomen; 29=head and thorax viewed from above; 30=last abdominal segments (Orig.)

of hind tibia and tarsi only slightly darkened, lateral side of tergite 1 partly dark reddish translucent. Frons only poorly shining, with minute punctures and also with rather dense larger punctures (Fig. 26). Punctures of mesonotum (Fig. 29) and

mesopleura distinctly deeper (Fig. 27) than on frons, denser on mesonotum and slightly scattered on mesopleura. Postscutellum only slightly impressed medially. Postnotum broad, finely wrinkled longitudinally laterally and scattered medially (Fig. 28). Propodeum moderately convex basally, surface finely granulated with shallow scattered punctures and with silvery pubescence. Last sternite strongly compressed laterally, apex of projecting apical part rather short and rounded (Fig. 30).

♂. — Unknown.

Specimen examined: Turkey: "Anatolien, Pozanti, SEIDENSTÜCKER 8.6.60" 1♀ holotype Hym. Typ. No. 3650 (Budapest).

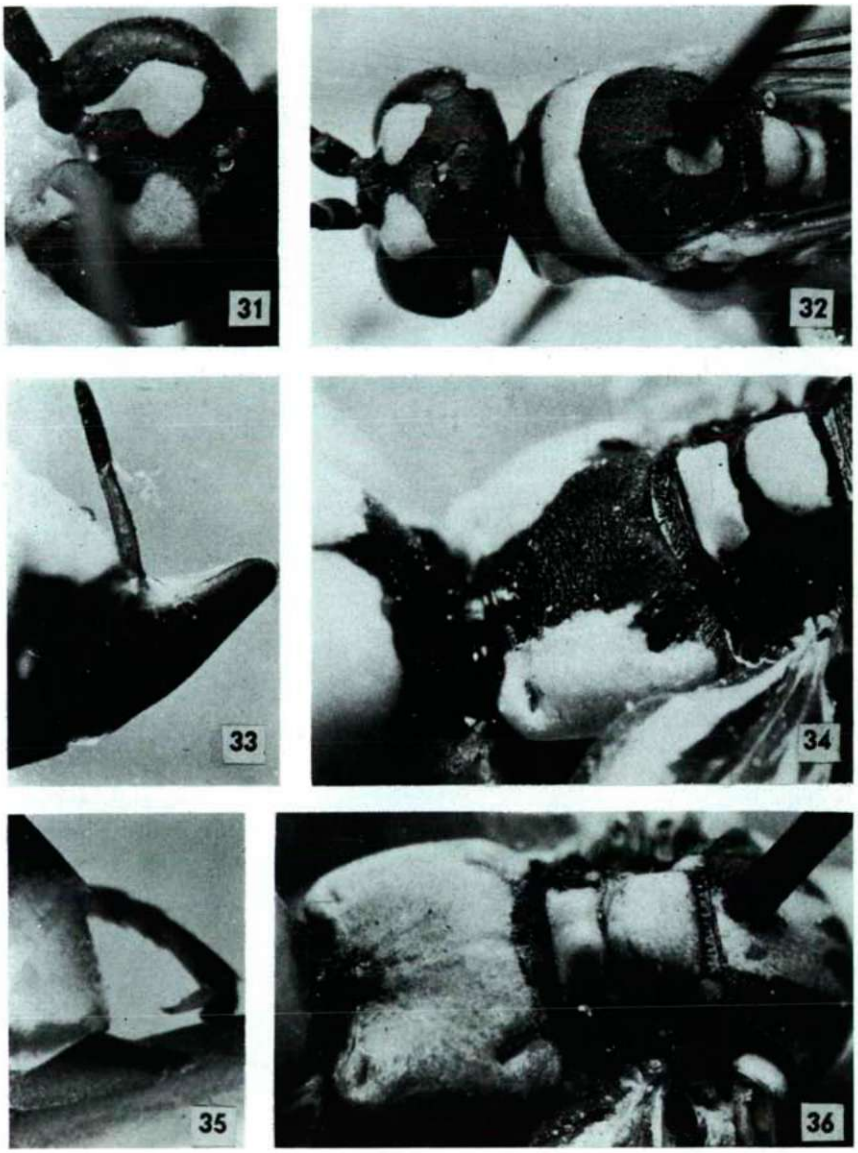
Related to *C. albicinctus albicinctus* ROSSI, but differs especially in its larger size, in its different light colour, e.g.: femora not completely rufous, mesopleura not with one ivory spot, light bands of tergites not narrow, punctures of body not shallow, etc.

I have named this subspecies in honour of the outstanding specialist of Pompiloidea. Mr. H. WOLF, Plettenberg (FR Germany).

Ceropales albicinctus mediterranicus ssp. n.

♀. — Length 8—9 mm. Black. Face below antennal sockets, clypeus, labrum, mandibles, inner and outer orbits broadly except on vertex, spots of inner orbits extending from emargination of eyes into large circular spots towards centre of frons (Fig. 31), lower side of antennal joints 1—2, posterior — lateral margins and a spot on front callus of pronotum, tegulae, scutellum and postscutellum, a spot on mesonotum (Fig. 32), two large spots on propodeum laterally (Fig. 34), a very small spot at basis of hind wings, a large spot at hind corner of mesopleuron, broad bands on tergites 1—6 posteriorly, only tergite 1 with a black excision medially (Fig. 34), sternites 2—5 with small spots laterally, underside of coxae and femora largely except black basis, partly also inner side of middle and hind ones, outer side of fore and middle tibia, as well as, metatarsi, yellow; antennal joints 3—12 rufous with moderately infuscated upper side, inner side of all femora, fore and middle tibia, as well as, tarsi partly rufous except a small basal spot, which is yellow. Frons mat, hardly shining, with fine very dense punctures and with some larger scattered and very shallow punctures (Fig. 31); ocelli forming an acute angle; punctures of pronotum, mesonotum and mesopleura deep and dense (Fig. 32), more scattered only on mesonotum laterally and on mesopleura. Postnotum slightly broader medially than laterally, with fine longitudinal wrinkles around deeper short impression in the middle and also with some fine transversal wrinkles basally in the middle (Fig. 34). Propodeum distinctly convex on its basal one-fourth, here with fine silvery pubescens and laterally flat on its declivous three-fourths part medially (in lateral view), surface finely granulated basally and with fine wrinkles towards base of abdomen, sometimes also with traces of transversal wrinkles on declivous part, surface with scattered shallow larger punctures in yellow lateral spots. Last sternite strongly compressed laterally, gradually narrowed apically with rounded apex (Fig. 33).

♂. — Length 7.5 mm. Similar to female both in colour and in sculpture, but



Figs. 31—34. *Ceropales albicinctus mediterraneus* ssp. n., 31 = head (holotype); 32 = head, pro- and mesonotum (holotype); 33 = last abdominal segments (paratype); 34 = scutellum-propodeum (paratype). — Figs. 35—36. *C. albicinctus seraxensis* RADOSZKOWSKI, 35 = last abdominal segments; 36 = mesonotum — propodeum (Orig.)

differs as follow: lateral small yellow streak not connected with lower large spot on pronotum and tergite 7 also yellow, upper side of antennal joints 3—13 rufous, hardly infuscated. Propodeum with rather deeper punctures laterally in yellow lateral spots.

The colour of this subspecies is uniform only in Cyprus, differs more on less from those from Morocco to Turkey as follows: the large spot on mesonotum absent in Spain and partly in Morocco, the spots of inner orbits extend from the emargination of the eyes only in a small degree and inner side parallel in Sardegna, Spain, Algeria and Morocco. Legs without rufous spots in Spain and partly (!) in Morocco. Black spots present on the basis of coxae usually and on trochanters (Sardegna, Morocco ♀ = Tetuan, not in ♂), trochanters black and black spots on base of femora (Turkey, Cyprus, Spain and partly Morocco ♂), trochanters and femora rufous on specimens from Algeria. One female from Morocco with completely rufous antennae, only the last joints darkened on upper side and 1 ♂ from Morocco the same but the joints 1—2 darkened above. There is 1 ♀ from Morocco with the whole upper surface darkened.

Specimens examined: Cyprus: "Zakaki Cyprus 19.6. 1936 leg. MAVROMOUSTAKIS" 1 ♀ holotype (Leiden); "Zakaki Cyprus 24. 6. 1936 leg. MAVROMOUSTAKIS" 1 ♂ allotype Hym. Typ No. 3651 (Budapest); "Zakaki Cyprus 29. 6. 1936 leg. MAVROMOUSTAKIS" 1 ♀ paratype Hym. Type No. 3652 (Budapest); "Cyprus Yermasogia River 22. 7. 1966 leg. MAVROMOUSTAKIS" 1 ♀ paratyp. Hym. Typ. No. 3653 (Budapest); "Cyprus Limassol 7. 6. 63" 1 ♀ paratype (Leiden). — TURKEY: Antakya 5. VI. 1965 1 ♀ SCHWARZ (Budapest). — Sardegna: Porth Torres 6. VI. 1952 1 ♂ CERESA (Budapest); Ploaghe 9. VI. 1952 1 ♀ CERESA (Zürich). — Spain: Las Correderas (Jaén) 600 m 17. VI. 1961 (MALAISE trap) 1 ♀ exc. RMNH (Budapest). — Tunesia: Tunis 1 ♂ SCHMIEDEKNECHT (Budapest). — ALGERIA: 2 ♂ (Budapest); Mascara 1 ♀ ROTH (Zürich); Mascara 12. VI. 1908 1 ♀ (Budapest). — Morocco: Tetuan 8. VI. 1955 1 ♀ ANDRADE (Zürich), 1 ♂ (Budapest). (Fig. 37).

In sculpture the subspecies is similar to *C. albicinctus albicinctus* ROSSI but the colour richer yellow and not ivory. It differs from *C. albicinctus seraxensis* RADOSZKOWSKI chiefly that its abdomen is never completely yellow, tergites always with black bands anteriorly and never with rufous spots; vertex never yellow or rufous behind ocelli; head, thorax with less yellow.

Distribution: Widely distributed but occur sporadically in Turkey, Cyprus, Sardegna, Spain, Tunesia, Algeria and Morocco.

Ceropales albicinctus seraxensis RADOSZKOWSKI

Ceropales histrio F. var. *seraxensis* RADOSZKOWSKI, 1893, Trudÿ russk. ent. Obshch., *27*:61 ♀
Ceropales albicincta ssp. *seraxensis:* 1931, GUSSAKOVSKIJ, Ann. Mus. Zool., *32*:5,14 ♀♂.
Ceropales albicinctus ssp. *seraxensis:* 1947, BEAUMONT, Mitt. Schweiz. Ent. Ges., *20*:517.

Specimens examined: Ukrainian SSR: Askanija-Nova 17. VII. 1924 1 ♀ GUSSAKOVSKIJ (Budapest). — Azerbaidzhan SSR: ACCP Sabirabad 23. VII. 1928 1 ♂ (Budapest). — Iran: Persia 1 ♀ (Budapest). — Turkmen SSR: Ashabad 1 ♀ AHNGER (Leningrad); Imam-baba 1 ♂ (Leningrad). — Uzbek SSR: Jargak Katorg 19. VI. 1926 1 ♀ GUSSAKOVSKIJ (Leningrad); ? Dabverzanyek 12. V. 19 27 1 ♂ (Budapest); Kuropatkino 18. V. 1930, 29—30. VII. 1930, 12. VIII. 1930 11 ♀ 1 ♂ GUSSAKOVSKIJ (Leningrad), 3 ♀ 4 ♂ (Budapest); Khiva, Ravat 20. V. 1927, 27. VII. 1927 1 ♀ 1 ♂ (Leningrad). — Tadzhik SSR: okr. Kulyaba 24. VII. 1933 1 ♂ POPOV (Leningrad); 1 ♀ (Budapest); Stalinabad, Dušambe 28. VII. 1934 1 ♀ GUSSAKOVSKIJ (Budapest). — Kazakh SSR: Semipalatinsk 1 ♀ (Leningrad). (Fig. 37).

This subspecies is similar to *albicinctus albicinctus* ROSSI sculpturally but differs by the extent of yellow spots and bands. Usually light yellow: nearly the whole

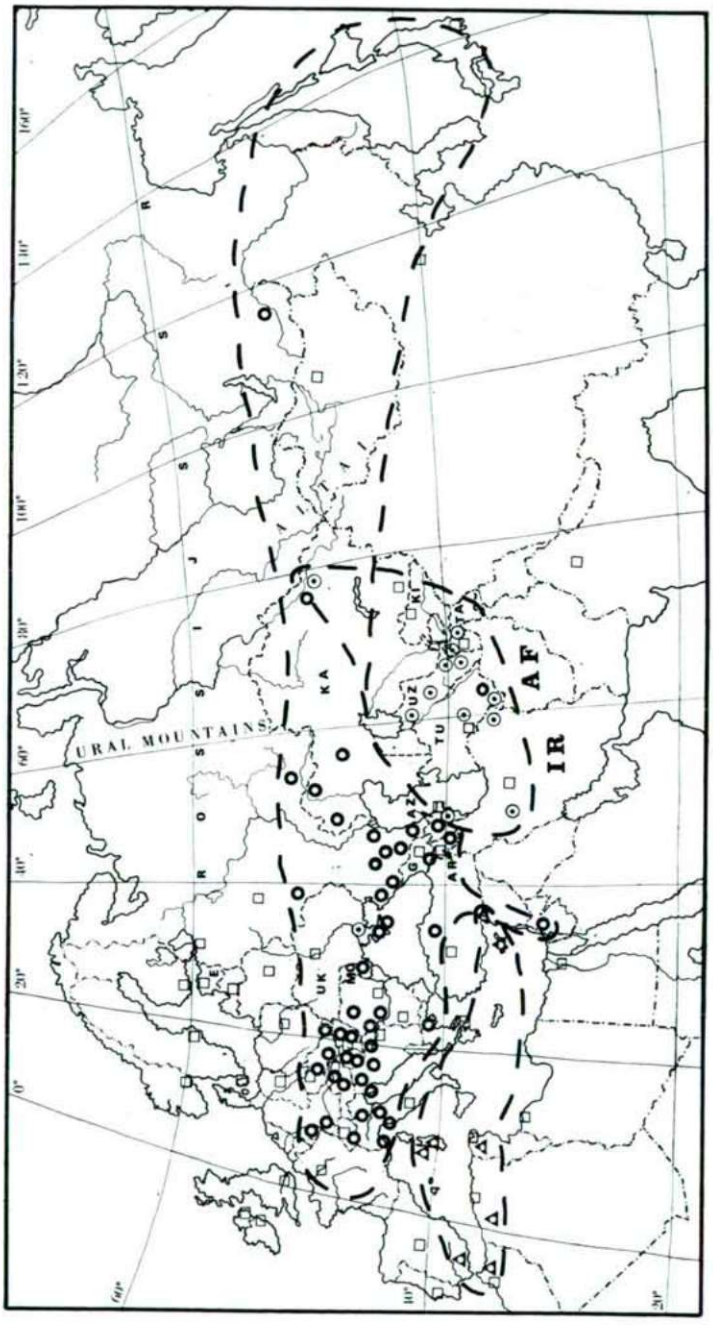


Fig. 37. The distributions of *Ceropales albicinctus albicinctus* Rossi, of *C. albicinctus mediterranicus* ssp. n. and *C. albicinctus seraxensis* Radoszkowski according to the data given in the text (Orig. by A. Fazekas)

pronotum and tergite 1, sometimes whole abdomen and propodeum largely, very often with rufous spots on tergites 1—2. Large yellow spots on mesonotum, scutellum, postscutellum (Fig. 36) and on lateral sides of mesopleura. Lower face yellow, the spots of inner orbits extend from the excision of the eyes into large pointed spots toward the centre of the frons, these spots are more reduced on specimen from the Ukrainian and Iran. The rufous spots are only translucent on specimen from the Ukrainian SSR and Iran or also on coxae and mesopleura (from the Ukrainian SSR) present and was not found in Turkmen SSR. Legs completely light yellow or partly rufous especially on the inner side of hind femora or on hind tibia. Small black spots may be present only at the base of coxae and trochanters. Antennae usually yellowish rufous, sometimes with very small black spots on upper side of joints 1 (Turkmen SSR), 1—2 (Tadzhik SSR) and only moderately darkened (on specimen from the Ukrainian SSR and Iran). Last sternite strongly compressed laterally and gradually narrowed apically with rather sharp pointed apex (Fig. 35).

Distribution: Chiefly in Uzbek-, scattered in Turkmen-, Ukrainian-, Azerbaidzhan-, Tadzhik-, East Kazakh SSR and Iran.

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TWO NEW SPECIES OF MESITINAE FROM EGYPT (HYMENOPTERA: BETHYLIDAE)

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Abstract

Two new species: *Anaylax aegyptius* sp.n. ♀ and *Heterocoelia priesneri* sp.n. ♂ are described from Egypt.

A material originating from Egypt sent kindly to me by Dr. K. V. KROMBEIN (Washington) included two new species who e descriptions follow hereunder.

Anaylax aegyptius sp. n.

♀. — Length 2.3 mm. Light yellowish brown; only flagellum, mesonotum, central areas of propodeum somewhat darker; abdomen black, base dark reddish translucent. Wings normal developed, reaching nearly to end of abdomen (Fig. 1), fore wings weakly brownish infuscated, with hyaline spot at base, outside of cells and at apex. Body sparsely covered with silvery hairs.

Head distinctly narrowing towards mouth parts, nearly as long as broad (19:22), remarkably broadened behind eyes, lateral sides nearly parallel, lateral corners rounded, posterior margin slightly arched with darker, narrow occipital carina, surface of head finely granulated only with few fine, shallow and hardly visible punctures, frontal sulcus developed only basally; ocelli forming an acute angle, POL: OOL=4:5, outer margins of ocelli with narrow grooves; anterior margin of clypeus protruding and rounded laterally, lateral sides parallel, surface raised into a high sharp keel medially; eyes small and moderately convex, elongated, its length and breadth ratio as 6:5, separated from mandibles by an equal distance of its length (6); antennae hardly thickened medially, joint 2 remarkably longer than 3, joints 4—9 quadrate, length (and breadth) proportions of antennal joints 1—13= = 9(3):4.5(1.8):3(2):2(2):2(2):2.5(2.5):2.5(2.5):2.5(2.5):2.2(2):2(1.5):2(1.5):2(1.5): 4(1.5). Pronotum three-fourths as long as broad in front, anterior corner finely rounded, lateral sides parallel only in front and diverging before tegulae, posterior margin narrowly impressed (Fig. 1), longitudinal furrow only very weakly developed, hardly visible, surface finely shagreened, shining. Mesonotum and scutellum finely shagreened, shining, longitudinal furrow of mesonotum not developed, parapsidal furrow hardly distinct, notauli deep. Mesonotum well separated from scutellum by a transversal groove and by a pair of small pits at its base laterally. Scutellum smooth without a longitudinal furrow basally. Propodeum remarkably long, distinctly longer than its half diameter (8:7), lateral spines of propodeum short (Fig. 1), only one-quarter as long as propodeum medially (2:8), all carinae developed, sublateral

area finely transversally striated, breadth of central: sublateral: lateral carina = =3.5:2.5:1. Lateral side of propodeum transversally wrinkled. Episternum coarsely punctured, with a transversal deep groove below tegulae. Abdominal tergites polished, shining, tergite 2 alutaceous basally, with only some fine scattered punctures medially (Fig. 1), tergites 3—6 polished.

♂. — Unknown.

Specimen examined: "Meadi 14.6.33", "Coll. Alfieri Egypt", 1♀ holotype (Washington, USNM Type No. 75491).

The new species is related to *Anaylax pillaulti* MÓCZÁR, 1970 and to *A. helleni* MÓCZÁR, 1970, I give the differences in the modified key of MÓCZÁR (1970a:179):

1—5a Text remains unchanged (MÓCZÁR 1970a: 178—179).

5b Longitudinal furrow of pronotum also shallow but developed only distally. Abdominal tergite 2 with scattered distinct or fine punctures and only basally shagreened 6

6 Antennal joints 2—3 of equal length. Lateral spines of propodeum stout, broad basally and acute apically, lateral sides of propodeum distinctly diverging backwards. Half diameter of propodeal disc distinctly broader than long transversally (10:8). Head, thorax brownish red, abdominal segments yellowish brown translucent. 3.5 mm *pillaulti* MÓCZÁR

— Antennal joint 2 clearly longer than 3. Lateral spines of propodeum slender, with narrow basis. Half diameter of disc equal or shorter than its medial length 7

7 Wings short, reaching to segment 1. Abdominal tergite 2 with scattered and fine punctures. Antennal joint 2 twice longer than broad. Malar space narrower than eye (6:8). Half diameter of propodeal disc transversally nearly equal to its medial length (7.5:7). Head, thorax yellowish brown, face and propodeum darker. 2.5—3 mm *helleni* MÓCZÁR

— Wings normal developed, reaching nearly to end of abdomen (Fig. 1). Abdominal tergite 2 only with some fine scattered punctures. Antennal joint 2 more than twice longer than broad. Malar space equal to length of eye (6:6). Half diameter of propodeal disc shorter than its medial length (7:8). Head, thorax light yellowish brown. 2.3 mm *aegyptius* sp. n.

Heterocoelia priesneri sp. n.

♀. — Unknown.

♂. — Length 4.2 mm. Black; mandibles, mouth parts, clypeus, malar space, lower face, first joints of antennae, vertex with ocelli and temples yellowish brown, partly yellowish red, pronotum light yellowish brown, mesonotum, scutellum and tegulae yellowish red except narrow black stripe at base of mesonotum, legs dark brownish red, abdominal segment 1, lateral side of tergite 2 dark reddish, last segments brownish. Wings normal, fore wings slightly brownish infuscated, with hyaline base, with a spot outside of cells and at apex. Veins brown. Body sparsely covered with short white hairs, only antennae with extremely long erect hairs (Fig. 4).

Head round, as long as broad (35:35), strongly thickened and moderately convergent behind eyes (Fig. 2), occipital margin distinct, ocelli forming an acute angle, POL:OOP=7:8, outer margins of ocelli with deep grooves; frontal sulcus

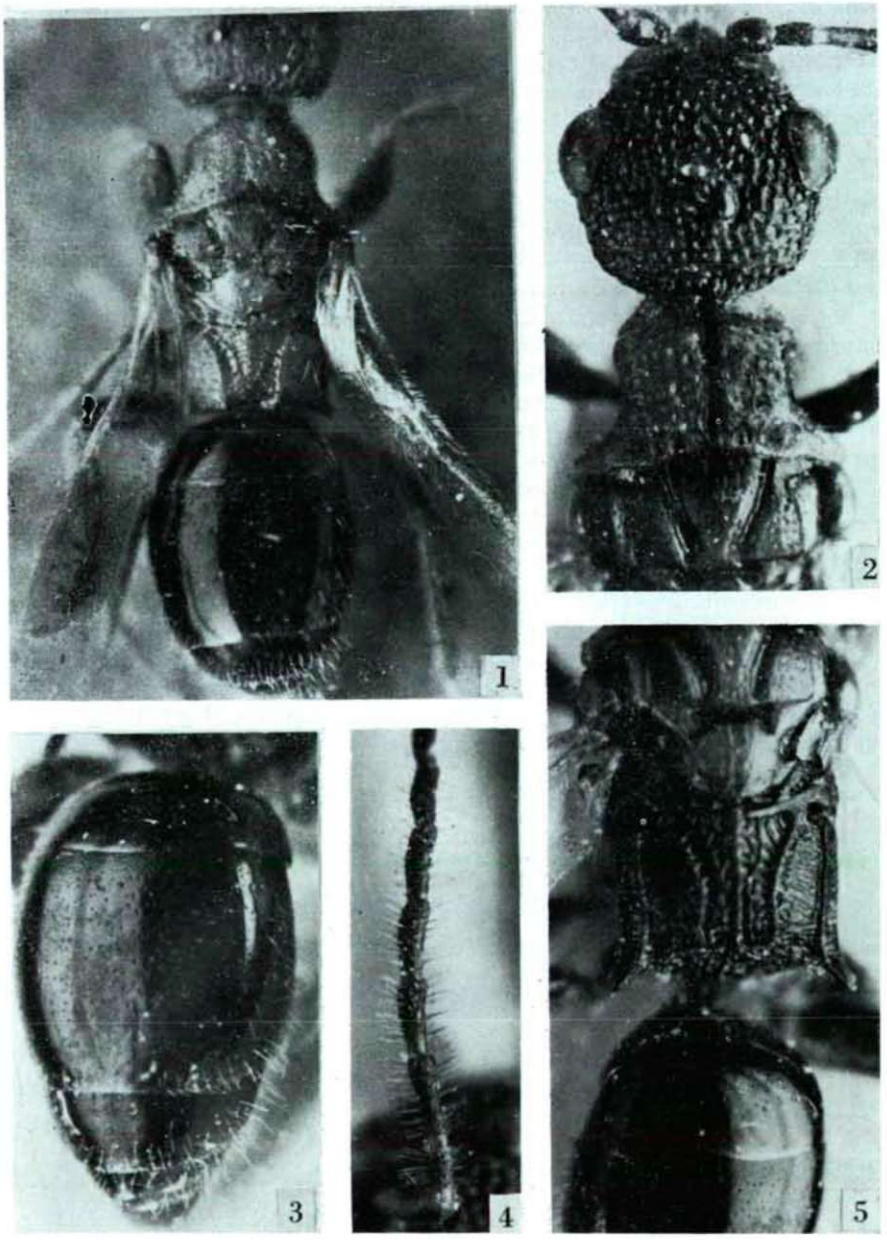

Fig. 1. *Anaylax aegyptius* sp. n. — Fig. 2—5. *Heterocoelia priesneri* sp. n., 2= head, pro- and mesonotum, 3=abdomen, 4=anterior antennal joints, 5=mesonotum, propodeum and anterior part of abdomen (Original).

present only basally, surface of head shagreened, densely and towards tempora and vertex gradually more deeply punctured; eye very convex, elongated, its length and breadth ratio as 13:11, separated from mandible by about two-thirds distance of its length (8:13); anterior margin of clypeus broadly rounded, surface raised longitudinally in a rather high sharp keel medially; antennae long and slender, joint 3 remarkably long, nearly twice as long as joint 2, antennal joints 1, 3—13 about three times longer than their diameter apically, joints 2—5 narrower proximally than distally, inner side of joints 4—8 concave, outer side of joints 4—9 convex, length (and breadth) proportions of joints 1—13=12(4):6(3):11(3):9(3):8(3):9(3): 9(2.5):8(2):7(2):7(2):6(2):6(2):9(2). Pronotum shorter than its breadth (16:22), lateral corners sharp, lateral sides nearly parallel in front (Fig. 2), strongly divergent only before tegulae, posterior margin broadly emarginated with a row of larger punctures, longitudinal sulcus narrow, deep, ending in a large pit before posterior margin, surface with distinctly larger and deeper punctures than on head, only weakly shining; mesonotum finely alutaceous with scattered fine punctures, shining, parapsidal furrow only slightly developed, notauli very deep and broad, mediolongitudinal furrow not developed (Fig. 5). Mesonotum separated from scutellum by a deep and narrow groove and by deep pits laterally. Scutellum alutaceous, shining with some small punctures, mediolongitudinal furrow shallow. Half diameter of propodeum about three-fourths as broad as its length medially (12:16), all carinae distinct, lateral angles with short but acute spines (Fig. 5), spine slightly longer than one-third length of propodeum (6:16), sublateral area very finely transversally wrinkled, breadth proportions of central: sublateral: lateral areas = =4.5:6.5:3. Episternum roughly sculptured with a transversal groove below tengulae. Abdominal tergite 1 polished only with few very fine scattered punctures (Fig. 3), tergite 2 alutaceous basally, with fine and scattered punctures medially and polished posteriorly (Fig. 3), tergite 3—4 alutaceous.

Specimen examined: "Choubrah 25.5.12", "Coll. Alfieri Egypte", 1♂ holotype (Washington, USNM Type No. 75492).

This species is easily recognizable by the antennal joints with long erect hairs from all known *Heterocoelia* species.

Sulcomesitius africanus MÓCZÁR

Sulcmesitius africanus MÓCZÁR, 1970b, Acta Zool. Acad. Sci. Hung., *16*:421, ♀

Specimen examined: Kerdasa, Sunt, 19.11.35, Egypt, Coll. R. MABROUK (Cairo Min. Agric.) 1♀ (without a head).

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COMPARATIVE EVALUATION OF PATHOLOGICAL AVAR FINDINGS FROM EXCAVATIONS BETWEEN THE DANUBE AND TISZA RIVERS

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Abstract

We have analysed the pathological deformations observed on 434 skeletons of five Avar cemeteries from the Danube-Tisza Interstream Region. The diagnosis of pathological findings is relying on earlier literary data and present-day investigations. The deformations of most frequent incidence are: osteoarthrosis and spondylosis derformans, as well as the initial and grave stages of cribra orbitalia. Clinical pictures of rarer incidence are: spondylitis tuberculosa, myeloma multiplex, aneurysma and bone metastasis. The examination of the pathological findings of the same archaeological age does not always refer to an identical way of life and the conditions of life in that age. We can only conclude the incidence, frequency and course of the clinical picture in a given from certain diseases.

Introduction

The pathological analysis completes the investigation into the historical populations carried out with the traditional anthropological methods, by adding one of the links in the chain leading to the biological reconstruction. And in addition to this, it enable us, as well, to establish of the series showing the corresponding anatomical variations, developmental anomalies — owing to the coincidence of anomalies — that the individuals may supposedly have been even in a closer connection with one another (ANDERSON, 1966; GRÜNEBERG, 1963). It is problematical, however, whether we may conclude from the parallelism of the pathological deformations in the stricter sense of the word, manifested in the skeletons, and from their occurrence in masses, an identical form of life or a genetic connection. For investigating this, we have evaluated the finds of five cemeteries from the age of Avars from pathological point of view.

Materials and Methods

The five series from the age of Avars, selected from the plain between the Danube and the Tisza rivers (apart from Hungary including Yugoslavia, as well), lie geographically close enough to one another. Most of these are already elaborated by means of metric, taxonomical and pathological methods (the missing pathological examination is contained in the present paper). There are to be enumerated the following items.

1. Mélykút-Sáncdülő: the early Avar cemetery with 45 graves, characterized by archaeological furniture, is anthropologically and archaeologically equally very important. It is a fully excavated cemetery. Its characteristic is that, apart from the early Avar graves, some graves with Sarmatic goods were also found, chronologically agreeing on the basis of the quotient of decomposition. The numbers of males, females and children are: 17, 22, resp. 6. They are taxonomically Europid, the Mongolid great race has only a single representative (MARCSIK, 1971). On the basis of the cemetery map, there could be supposed only two large families within which chronological differences and, on the basis of blood-group quality, family relations can be demonstrated (FARKAS—LENGYEL—MARCSIK, 1971). This fact is supported by the archaeological graves furniture, as well (KŐHEGYI—MARCSIK, 1971). The pathological elaboration of the cemetery took only place partially within the general anthropological elaboration (MARCSIK, 1971). Completing this with the present investigations, we have to mention the following major morhological and pathological deformations: the processus temporalis ossis sphenoidalis — as a peculiar anatomical variation —, the spina bifida — classified among malformations (in sacrum and atlas equally) — the sacralisation, the openness of the foramen transversarium, and the spondylolysis. From among the pathological deformations in the strict sense of the word we have to emphasize — as they occur in the skeleton — the osteoarthrosis (at the articular surfaces of vertebrae but at the epiphyses of the long bones, as well) and the spondylosis deformans (in the cervical, lumbal, thoracal sections equally). The porotic form of cribra orbitalia can only be seen in five crania. Status post fracturam is only to be observed in the skeletons of three males (in one of the cases accompained by a strong callus-formation while in the other two cases by osteomyelitis). In the caput femoris of the young-age left femur from grave 28 a cavitation can be seen, with a diameter of 1 cm, lying one and half cm from the surface. The gap begins in the fovea capitis femoris, there is a similar resoptive cavity also in the fuga of epiphysis but this is smaller. In the left fossa acetabuli two major circular openings are to be observed. In the right femur there is to be seen no similar deformation. This cavitation may have been, very probably, the result of a bone process of tuberculotic origin (HARANGHI, 1966). The process itself may have begun at the enlarged double opening of the fossa acetabuli, following the line of the ligamentum teres femoris, more exactly that of blood vessels running in this which have an intensive part in feeding the head of the thigh. Osteoporosis generalisata can be seen in more than one skeleton but these are from the older age, their significance may, therefore, be neglected.

2. Kunszállás-Fülöpjakab: the metric-taxonomical examination of 50 skeletons of the cemetery with rich grave furniture from the late age of Avars was performed by LIPTÁK—VARGA in 1971. It is a series of Mongolid and Mongoloid preponderance (11 males, 21 females, 18 of undetermined sex). The results achieved by analyzing the inorganic matter of bones (VARGA, 1971) supported the diagnosis of pathological processes (VARGA—MARCSIK, 1975). It is to be seen from Table 1 of the latter monograph that in the series seven kinds of deformations are confined to 21 cases and affect 10 skeletons (three males, seven females). These seven kinds of deformations are as follows: spondylosis deformans, arthrosis deformans, spondylarthrosis (osteoporomalacia, senilis atrophia), block vertebra, status post fracturam anomalies. The deformations of arthrosis manifest themselves in the bones found in the cemetery at Kunszállás in an extremely grave form. The

cribra orbitalia, not characterized in this paper, are limited to an obviously low number of cases, not more than three (two males and one female), in porotic and cribrate forms. Eight of the ten skeleton's graves are located beside one another in the cementery map. This phenomenon, as well as the connection according to the determination of blood groups permit to suppose that the eight individuals may have been in blood-relationship with one another.

3. Süköd—Ságod: the skeletons of 165 graves of the cemetery, medium rich in archaeological grave furniture, were elaborated. On the basis of the grave goods, this matter forms a transition between early and late Avars. The beginning of the cemetery may have been between the years 640 to 660 while in the middle of the 8th century the buryings already ceased to continue. From among these 41 are males, 68 are females and 56 are children. It is a cemetery of mostly Europid character; the Mongolid element can be demostrated in four cases. But taxonomically, there could only be diagnostized a single Mongolid cranium (KŐHEGYI—MARCSIK, 1971a). The cemetery is extremely interesting from pathological point of view, what is confirmed by a series of papers published (MARCSIK, 1972; KŐHEGYI—MARCSIK, 1976; MARCSIK, 1975; MARCSIK—KÓSA, 1976, 1976a). It is shown by these papers that, apart from several anatomical variations and developmental anomalies (atlas manifestation, open canalis caroticus), some characteristic deformations may also be found. Thus the spondylitis tuberculosa (1 case), accompanied also by coxitis tuberculosa, as well as the primitive and the fully express forms of the cribra orbitalia (hyperostosis spongiosa orbitae). This latter was observed at three children, at one of them, however, also the hyperostosis spongiosa cranii is present. In one case, also the characteristic cranial deformation of the myeloma multiplex is remarkable while in another case a longer recess at the internal surface of the cranium — supposedly as a result of an aneurysm. In addition to these, in a few cases, osteoarthrosis and spondylosis deformans also occurred. In two cases, we have observed the characteristic necrosis of the processus of the mandibula.

4. Baja — Dózsa György street: neither its archaeological nor its anthropological elaboration has taken place. It turned out from the excavation record (and I wish to express here my thanks to M. KŐHEGYI for having made the excavation record and map available to me (that not more than ten graves of a late Avar cemetery could be rescued. The sex and age of life determination of the ten skeletons, as well as their pathological examination, are contained in the present paper. The number of males is four, that of females three and that of children the same. Although the metric-morphotaxonomical determination of skeletons has not taken place, we could establish definitely that, two femals are Mongolid for sure, while the other adults are Europid. According to the pathological investigation performed, in this small series the primitive and grave outward forms of the cribra orbitalia are to be emphasized. Their division is shown in the following summary.

The different formations of cribra occurred, therefore, in four cases of the ten finds. In the cranium showing hyperostosis spongiosa orbitae, some deformations referring to rachitis can also be recognized (the tuber frontalis and parietalia protrude more, giving a characteristic cubic shape to the skull). The graves of skulls, showing different degrees of cribra, are localized in the cemetery map close to one another. (In addition to, in one case, the traces of osteoarthrosis are also to be seen in the vertebra.

Cribra orbitalia		Inf. I.	Inf. II.	Juv.
porotic	with similar deformation in the os frontale	—	—	1
	with hyperostosis spongiosa cranii	—	1	—
cribrate		—	1	—
hyperostosis spongiosa orbitae (with further porotic areas of the cranium)		1	—	—

5. Bačka-Topola: In Yugoslavia, in findspot Bačka-Topola near Subotica, 202 graves were excavated, 33 of these being of Sarmatian age. According to the oral communication of the archaeologist L. SZEKERES, these are comparatively rich in grave furniture. Age of life and sex were determined by GY. FARKAS. In his opinion, from the 164 finds examined 57 are males, 65 females while the number of children is 42. Taxonomically — provisorily — they are mostly Europo-Mongolids, Mongolids. As in the skeletons a great many anatomical variations, pathological deformations can be observed, thus the elaboration and detailed evaluation of these both took place (FARKAS—MARCSIK—VÉKONY, 1976; FARKAS—MARCSIK, in press; FARKAS—HUNYA—MARCSIK, 1978; MARCSIK—FARKAS, in press). Within the anatomical variations, developmental anomalies, the incidense of torus mandibularis, the opennes of the canalis caroticus, the appearance of the spondylolysis, the "cleft" vertebra and spina bifida are very important. From among the graver pathological deformations there are obvious in three skeletons the spondylitis tuberculosa, in more than one case the different degrees of spondylosis deformans (with block-formation), of arthrosis deformans, as well as of cribra orbitalia) in one of the cases hyperostosis spongiosa cranii is also visible). The osteolytic and osteoplastic of the multiplex incidence of a metastatic process is discernible in the skeleton of a male but there cannot be observed any deformation in the skeleton refferring to a primary tumour. The gibbus-formation owing to the above-mentioned progress of disease (spondylosis deformans, spondylitis tuberculosa), the great frequency of osteoporosis (accompanied mostly by fishshaped, resp. wedge-shaped vertebrae), the strong osteophyte-formation in the vertebral body, the regular grouping of developmental anomalies in the cemetery map are refferring to an identical form of life and a closer community. The high number of the pathological deformations in the series is interesting in itself and presupposes endogamy.

Discussion

We have analysed the pathological deformations observed on the 434 skeletons originating from the Danube-Tisza Interstream Region (130 males, 179 females, 125 undetermined and children). The diagnosis of our pathological findings is relying on earlier literary data and present investigations. In the course of the latter ones, we also arrived at general anthropological conclusions. Thus:

1. The value of the Collo-diaphysis angle — used for differentiating sexes — demands due circumspection. In the older age, its value declines, even irrespective of sexes: the area of the acetabulum facies lunata often merges into the fossa acetabuli. Therefore in the fossa acetabuli the traces of a denser vascular system, as distinguished from the average, or a quite deepened area of it can be observed. The fovea capitis femoris grew larger, became deepened. Therefore, in erderly age, the pelvic-femur joint gets into vara position, independently of sexes.

2. We know from Houghton's paper (1974) that sulcus praeauricularis is characteristic not only of females but a weaker expressed form of it can be found in the male pelvis, as well (indifferent sex character). We could confirm this statement in our own material, too.

Our earlier establishment that the hyperostosis spongiosa cranii may be considered as a graver outward form of cribra orbitalia, is justified, apart from the cemetery at Sükösd, also by the finds in Baja-György Dózsa street. On the basis of our investigation (MARCSIK—KÓSA, 1976; 1976a), in the aetiology of these we have supposed the disturbances of the haemopoietical system as a pathogenetic factor. ASCENZI (1976) is emphasizing in case of the form with hyperostosis the pathogenic role of thalassemia major, while EL-NAJAR et al. (1975, 1975a) are mentioning in their paper hypoferric anaemia as an aetoligical factor.

The brief summary of the pathological deformations occurring in the material of the five cemeteries investigated is given in Table 1. (It is, of course, made difficult to drow the conclusions by that, except for the cemetery at Mélykút, the other cemeteries are not fully excavated). On the basis of the investigations it turned out that, as to the pathological bone finding, there is generally no diffierence between males and females, with the exception of the cribra orbitalia (or porotic hyperostosis), seen most frequently in the crania of females and children.

It can be ascertained from the data of Table 1 that, with the exception of the finds in the cemetery at Mélykút, that in any case we meet rather the graver clinical picture. The cause of the difference is perhaps that this cemetery is an early Avar one while the others are from the later time of Avars or they are from a transitional age. We could, of course, draw consequences only after looking over several early Avar series. At comparing the pathological findings of Avar cemeteries, we have found some deformations, like the osteoartrosis and spondylosis deformans, occurring in all the five series. But from these two clinical pictures we could not draw any conclusions that would refer to an identical way of life. On the one hand, because the inflammatory as well as regressive processes of joints cannot be separated in a palaeoanthropological material with absolute certainty; on the other hand, because the morphological finding is also in case of spondylosis deformans the same but for its appearance innumerable aetiological and pathogenic factors may be responsible. Healed fractures were found, with the exception of the finds in Baja—Gy. Dózsa street, in the material of all the cemeteries. These can be evaluated if they occur in the form of an independent clinical picture. Similarly, the myeloma, aneurysma, bone metastasis, like rarely occurring clinical pictures, are significant at an analysis within the series.

The evaluation of the incidence of cribra orbitalia in masses already enables us to drow the conclusions connected with the investigation into aetiological factors. In this case if we accept the hypoferric anaemia like its aetiology then this refers to the general malnutrition of that age like an endemic disease. That is to say, it is

Table 1. Comparison of some Avar series

Findspot	Mélykút	Kunszállás	Sükösd—Ságod	Baja—Gy. Dózsa	Bačka-Topola
Archaeological age	early Avars	late Avars	early-late Avars	late Avars	early-late Avars
No. of skeletons examined	45	50	165	10	164
Taxonomical determination	Europid	Mongolid Europid	Europid Mongolid	Mongolid Europid	Mongolid Europid
Major pathological deformations	osteoarthrosis	osteoarthrosis*	osteoarthrosis	osteoarthrosis	osteoarthrosis*
	spondylosis deformans	spondylosis deformans	spondylosis deformans	—	spondylosis deformans*
	cribra orbitalia	cribra orbitalia	cribra orbitalia*	cribra orbitalia*	cribra orbitalia*
	fractura	fractura	fractura	—	fractura
	—	myeloma multiplex?	myeloma multiplex	—	—
	—	—	aneurysma?	—	—
	tbc?	—	tbc*	—	tbc*
	—	—	—	—	metastasis*

* The deformations indicated with "*" manifested themselves in an express form.

characteristic of the general living conditions in that time. And if we consider the thalassemia or one of its kinds as an elicting factor then primarily genetic factors have a part in their induction.

The general way of life can be concluded from the appearance of bone tuberculosis only partially, taking into consideration that the pulmonary and enteric forms cannot be separated from each other.

The investigation into pathological findings of the some archaeological age do not always refer to the same way of life and the living conditions of that age. In the given case, the incidence, frequence and pathological process of the clinical picture can only be concluded from certain diseases.

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